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A REVISION OF THE SCALY TOADFISHES, GENUS *BATRACHOIDES*, WITH DESCRIPTIONS OF TWO NEW SPECIES FROM THE EASTERN PACIFIC

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ABSTRACT

Batrachoides differs from all other American genera of Batrachoididae in having the body covered with scales and in having two subopercular spines. Nine species are recognized: *liberiensis* (Steindachner) from the Gulf of Guinea (with *beninensis* Regan a synonym); *manglae* Cervigón from Venezuela; *gilberti* Meek and Hildebrand from the Caribbean side of the Yucatán Peninsula south to Panamá; *surinamensis* (Bloch and Schneider) from Honduras to Salvador, Brazil; *goldmani* Evermann and Goldsborough from Atlantic-draining streams in the Río Usumacinta and Río Grijalva in México and Guatemala; *boulengeri* Gilbert and Starks from the Bay of Panamá; *pacifici* (Günther) from Panamá to northern Peru; *waltersi* n.sp. from Acapulco, Mexico south to the Gulf of Nicoya, Costa Rica; and *walkeri* n.sp. known only from the holotype from the Bay of Panamá. *B. boulengeri* and *B. surinamensis* are a pair of Pacific-Atlantic geminate species as are *B. pacifici* and *B. gilberti*. *B. waltersi* is clearly related to *B. boulengeri* and *B. surinamensis* but has fewer dorsal and anal fin rays and vertebrae. *B. walkeri* is similar to *B. boulengeri* and *B. surinamensis* in small eye size and high vertebral and dorsal ray counts but differs from both in having reduced squamation on the head. Attempts to analyze relationships within the genus led to an unresolved trichotomy between *B. liberiensis*, the *B. boulengeri* species group (including *B. surinamensis*, *B. waltersi*, and *B. walkeri*), and the *B. pacifici* group (including *B. gilberti*, *B. manglae*, and *B. goldmani*). Brief notes are included on swimbladder morphology, fecundity, food habits, and parasites.

The purposes of this paper are to distinguish *Batrachoides* from other genera of toadfishes, diagnose the nine species that comprise the genus, two of which are described as new, discuss geographic variation in widespread species, and hypothesize relationships among the species. Brief notes are included on swimbladder morphology, fecundity, food habits and parasites.

METHODS AND MATERIALS

At the subfamily level, important taxonomic characters in the Batrachoididae include presence or absence of photophores and of hollow spines connected to venom glands (Smith, 1952; Collette, 1966). At the genus level, characters such as the presence or absence of scales and the nature of the glands around the pectoral fin region (Collette, 1966) are important. Other useful characters include number of vertebrae (precaudal and caudal), number of fin rays (dorsal, anal, and pectoral), number and shape of teeth, shape of anterior nostril tube (Roux, 1971), number of lateral lines, number of opercular and subopercular spines, and number and shape of barbels, flaps, and cirri on the head and body (Collette, 1974a). Within *Batrachoides*, meristic characters such as the numbers of pores in the upper and lower lateral lines, pectoral fin glands, dorsal and anal rays, and vertebrae and morphometric characters such as eye size are useful in separating species. Swimbladder morphology distinguishes one species from the others.

Morphometric data were treated in two different ways. The species descriptions include proportional measurements, i.e., one measure expressed as a percent of another. Minimum values, maximum values and arithmetic means are presented in tables to supplement the accounts of each species. In order to test for differences between species or between geographic populations within a species the analysis of covariance (ANCOVA) procedure was used. This procedure tests null hypotheses concerning 1) overall coincidence, 2) equality of slopes and, 3) equality of intercepts of two or more regression equations. If hypothesis 1 above was rejected at a prespecified level of significance (0.05 throughout this study) hypotheses 2 and 3 were then tested. If the null hypotheses concerning the slopes or intercepts of three or more groups were rejected we used the Newman-Keuls multiple range

test (MRT), in order to determine which regressions were different from others. It is not uncommon for the ANCOVA procedure to reject a null hypothesis and have the MRT procedure unable to detect differences. It is generally accepted that the ANCOVA procedure is a more powerful test than the MRT.

Meristic characters were analyzed for intraspecific variation using the single factor analysis of variance (ANOVA) procedure. If a difference at the 0.05 level of significance was detected between means, the MRT procedure was used to attempt to determine which mean values were different from others.

Statistical tests were performed on the IBM 370-148 computer at The George Washington University using computer programs written and maintained by the NMFS Systematics Laboratory.

All statistical procedures and notation used in this investigation follow those presented by Zar (1974), with the exception that the probability associated with the calculated value of the F statistic of the ANCOVA procedure is generated by the computer program and for the purpose of simplification and clarity is used instead of the calculated value of the F statistic with its associated numerator and denominator degrees of freedom. Unless otherwise stated, the independent variable used for all regressions is standard length.

All dorsal and anal fin ray elements were counted and counts were verified from radiographs. Vertebral counts were made from radiographs and include the two ural centra. Two factors cause difficulties in counting teeth; they are frequently broken or missing, leading to low counts when estimating the number of empty sockets; high counts result from counting extra replacement teeth. To arrive at the best estimate for the number of teeth on the premaxillary, palatine, and dentary bones, counts for left and right sides were averaged and rounded off to the nearer higher whole number. These averaged numbers are used in the species descriptions (except for the vomer, for which total counts are given). Papillae were counted along the dorsal lateral line from above the opercular spine to the caudal base and along the ventral lateral line from between the pectoral and pelvic fin insertions to the caudal base. Counts were recorded for the anterior and posterior portions of the lateral line and the ranges of both portions are included in the species accounts. The dividing point between anterior and posterior portions of the lateral line is where the papillae leave the lateral surface of the body and move close to the dorsal (or ventral) mid-line. The total number of papillae in each lateral line is also included in the species accounts and these totals are what are summarized in the tables. Standard length was measured from the tip of the upper jaw to the caudal base. Head length extends to the most posterior part of the opercular flap. Head width was measured at its maximum point. Orbit length is the maximum length of the orbit. Interorbital width is the least distance between the orbits. Snout to second dorsal and snout to anal are straight line distances to the origins of these fins. Pectoral fin length was measured from the upper base of the fin to the tip of the longest ray; pelvic fin length from the outer base to the tip of the longest ray.

Material examined is in the following collections: AMNH (American Museum of Natural History, New York); ANSP (Academy of Natural Sciences, Philadelphia); BMNH (British Museum (Natural History), London); CAS (California Academy of Sciences, San Francisco); FMNH (Field Museum of Natural History, Chicago); GCRL (Gulf Coast Research Laboratory, Ocean Springs, Miss.); LACM (Los Angeles County Museum of Natural History); MCZ (Museum of Comparative Zoology, Harvard University); MNHN (Muséum National d'Histoire Naturelle, Paris); NHMV (Naturhistorisches Museum, Vienna); SIO (Scripps Institution of Oceanography, La Jolla, California); SU (Stanford University, specimens now at CAS); UA (University of Arizona, Tucson); UCLA (University of California, Los Angeles); UCR (Museo de Zoología, Universidad de Costa Rica, San José); UDONECI (Universidad de Oriente, Nueva Esparta, Coleccion Ictiologia, Isla Margarita, Venezuela); UMML (University of Miami; Rosenstiel School of Marine and Atmospheric Science, Miami); UF (Florida State Museum, University of Florida, Gainesville); UMMZ (University of Michigan Museum of Zoology, Ann Arbor); UPR (University of Puerto Rico, Mayaguez); USNM (U.S. National Museum of Natural History, Washington); and WAM (Western Australia Museum, Perth).

Batrachoides Lacepède

Batrachoides Lacepède, 1800: 451 (type-species *Batrachoides tau* Lacepède, = *Batrachus surinamensis* Bloch and Schneider, not *Gadus tau* Linnaeus, by subsequent designation of Jordan and Evermann, 1896: 466).

Batrachus Bloch and Schneider, 1801: 42 (type-species *Batrachus surinamensis* Bloch and Schneider by subsequent designation of Jordan, 1917: 57).

Batrictius Rafinesque, 1815: 82 (substitute name for *Batrachoides* Lacepède and therefore taking the same type-species: *Batrachoides tau* Lacepède = *Batrachus surinamensis* Bloch and Schneider).

Diagnosis.—A genus of the subfamily Batrachoidinae (lacks hollow dorsal and opercular spines connected to venom glands and lacks photophores). Differs from

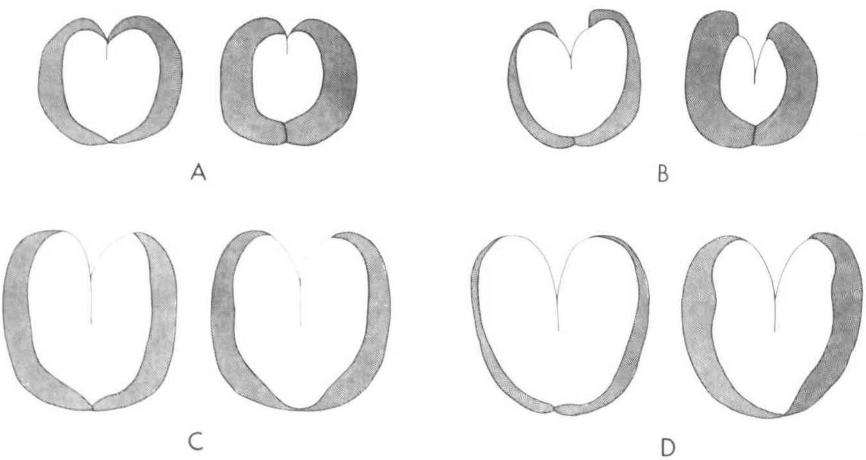

Figure 1. Swimbladders of two species of *Batrachoides* showing the deeper division between left and right lobes in *B. goldmani* compared to the other species of the genus, represented by *B. waltersi*. A. *B. waltersi*, female, 163 mm SL, USNM uncat. B. *B. waltersi*, male, 183 mm SL, UCLA W70-5. C. *B. goldmani*, female, 106 mm SL, USNM 219383. D. *B. goldmani*, male, 216 mm SL, USNM 50006. In each case, left figure is the swimbladder in ventral view, right in dorsal view. Stippling indicates the intrinsic swimbladder musculature.

all other American genera in having the body covered with scales and in having two subopercular spines (none in Thalassophryninae and Porichthyinae, one in other American genera). Lacks the axillary foramen present in *Opsanus* and *Sanopus* in the western Atlantic and *Halobatrachus* in the eastern Atlantic and the axillary pouch found in *Parabatrachus* in the eastern Atlantic. A gland is present in the axillary region as in *Amphichthys* (and *Porichthys*). No nasal barbels as are present in the other three genera found in the eastern Atlantic (*Halobatrachus*, *Parabatrachus*, and *Chatrabus*). Glands (2–19) present between the pectoral fin rays, as in *Triathalassothia* and *Opsanus*. Three dorsal spines, 22–29 rays; 20–27 anal rays; 18–23 pectoral rays; 9–10 precaudal vertebrae, 22–29 caudal vertebrae, 31–38 total; 30–64 pores in upper lateral line, 30–62 in lower.

Swimbladders of species of *Batrachoides* are similar to those of other genera of Batrachoididae such as *Opsanus* (Tower, 1908: fig. 4), roughly heart-shaped with an anterior division into two lobes and the intrinsic musculature in bands along the lateral surface of each lobe (Fig. 1).

Swimbladders were removed from at least one mature male and one mature female of each of the nine species of *Batrachoides* (except *B. walkeri* for which only one specimen, a mature female is available) for a total of 12 females and nine males. No sexual dimorphism was apparent in the musculature of the swimbladder. In order to determine if there is a difference in swimbladder shape between males and females of *Batrachoides*, a paired sample t-test ($n = 9$) was performed on the proportions length anteroventral groove divided by total swimbladder length and length anterodorsal groove divided by total swimbladder length. The calculated values of t (0.161 and 0.520, respectively) were not significant at the 0.05 level so we conclude that there is no sexual dimorphism in swimbladder shape. The division between left and right lobes is clearly deeper in *B. goldmani* (ventral division 56–63% total length of swimbladder, dorsal division 68–69%) than in the other species (ventral division 20–48%, dorsal division 21–64%). This difference is illustrated with *B. waltersi* representing the more common condition (Fig. 1).

Key to the Species of *Batrachoides*

1a. Usually fewer than 24 rays in second dorsal fin; usually fewer than 21 rays in anal fin; usually fewer than 34 pores in lower lateral line 2
1b. Usually 24 or more rays in second dorsal fin; usually 21 or more rays in anal fin; usually 34 or more pores in lower lateral line 3
2a. Pectoral fin glands 11 or fewer .... *B. manglae* (Venezuela)
2b. Pectoral fin glands 13 or more .... *B. goldmani* (Usumacinta-Grijalva drainage of México & Guatemala)
3a. Supraorbital filaments present 4
3b. Supraorbital filaments absent 6
4a. Interorbital filaments present 5
4b. Interorbital filaments absent .... *B. walkeri* n.sp. (Pacific coast of Panamá)
5a. Pectoral fin glands 8 or fewer .... *B. gilberti* (Caribbean coast of Central America)
5b. Pectoral fin glands 13 or more .... *B. liberiensis* (Gulf of Guinea)
6a. Interorbital filaments present 7
6b. Interorbital filaments absent 8
7a. Usually 52 or more pores in upper lateral line; usually 48 or more pores in lower lateral line; usually 16 to 18 pectoral fin glands .... *B. waltersi* n.sp. (Pacific Coast from México to Costa Rica)
7b. Usually fewer than 52 pores in upper lateral line; usually fewer than 48 pores in lower lateral line; usually 12 to 14 pectoral fin glands .... *B. pacifici* (Pacific Coast from Panamá to Peru)
8a. Scales on head extending just anterior to supratemporal canal (Fig. 2a); pectoral fin glands 16 or more .... *B. boulengeri* (Pacific Coast of Panamá)
8b. Scales on head extending beyond supratemporal canal to middle of head (Fig. 2b); pectoral fin glands 11 or fewer .... *B. surinamensis* (Caribbean & Atlantic Coasts of Central & South America)

Batrachoides boulengeri Gilbert and Starks

Batrachus surinamensis. Not of Bloch and Schneider. Günther, 1861: 174 (in part; Pacific coast of Central America).

Batrachoides boulengeri Gilbert and Starks, 1904: 182–184 (original description, Panamá Bay), pl. 31, figs. 57–57a. Meek and Hildebrand, 1928: 916–917 (description; Pacific coast of Panamá; 4 specimens, 301–352 mm SL, USNM 80989–92). Jordan, Evermann, and Clark, 1930: 487 (listed). Fowler, 1944: 525 (Panamá Bay; listed). Böhlke, 1953: 147 (type SU 6487).

Diagnosis.—The largest species of *Batrachoides* (maximum size 362 mm SL); with very small eyes (2.5–4.0% SL, $\bar{x}$ 3.20), 2.44–5.87 times in interorbital width ($\bar{x}$ 3.68); moderate head squamation (extending anteriorly just past the supratemporal canal, Fig. 2A); no supraorbital or interorbital filaments; many lateral line pores (upper (41–52) + (4–15) = 52–63, lower (31–42) + (12–17) = 47–56); many fin rays (dorsal rays 28–29, usually 29; anal rays 26–27, usually 26; pectoral rays 21–23); many vertebrae (usually 10 + 28 = 38); and many pectoral fin glands (16–18, rarely 19).

Body proportions are presented in Table 1, counts in Tables 2–5. Teeth on dentary 21–24, premaxilla 25–42, palatine 11–14, and vomer 6–10.

Very similar to *B. surinamensis* in large body size, small eye size, and high counts of most meristic characters but differs sharply in having many more pectoral fin glands (16–19 vs. 0–11) and in having the head squamation reaching anterior only as far as the supratemporal canal (instead of to the middle of the head). Differs from *B. waltersi* and *B. pacifici* in having more dorsal and anal fin rays and vertebrae (Tables 2 and 3).

Types.—Holotype CAS SU 6487 (1, 286); Panamá Bay; C. H. Gilbert and E. C. Starks; 1896; D III, 29; A 26; P_1 22; vertebrae 10 + 28 = 38; upper lateral line 46 + 13 = 59; lower lateral line 38 + 15 = 53; P_1 glands 18–17; head squamation extending forward slightly anterior to supratemporal canal; no supraorbital tentacle over right eye, a tiny filament over left eye; no interorbital filaments; head

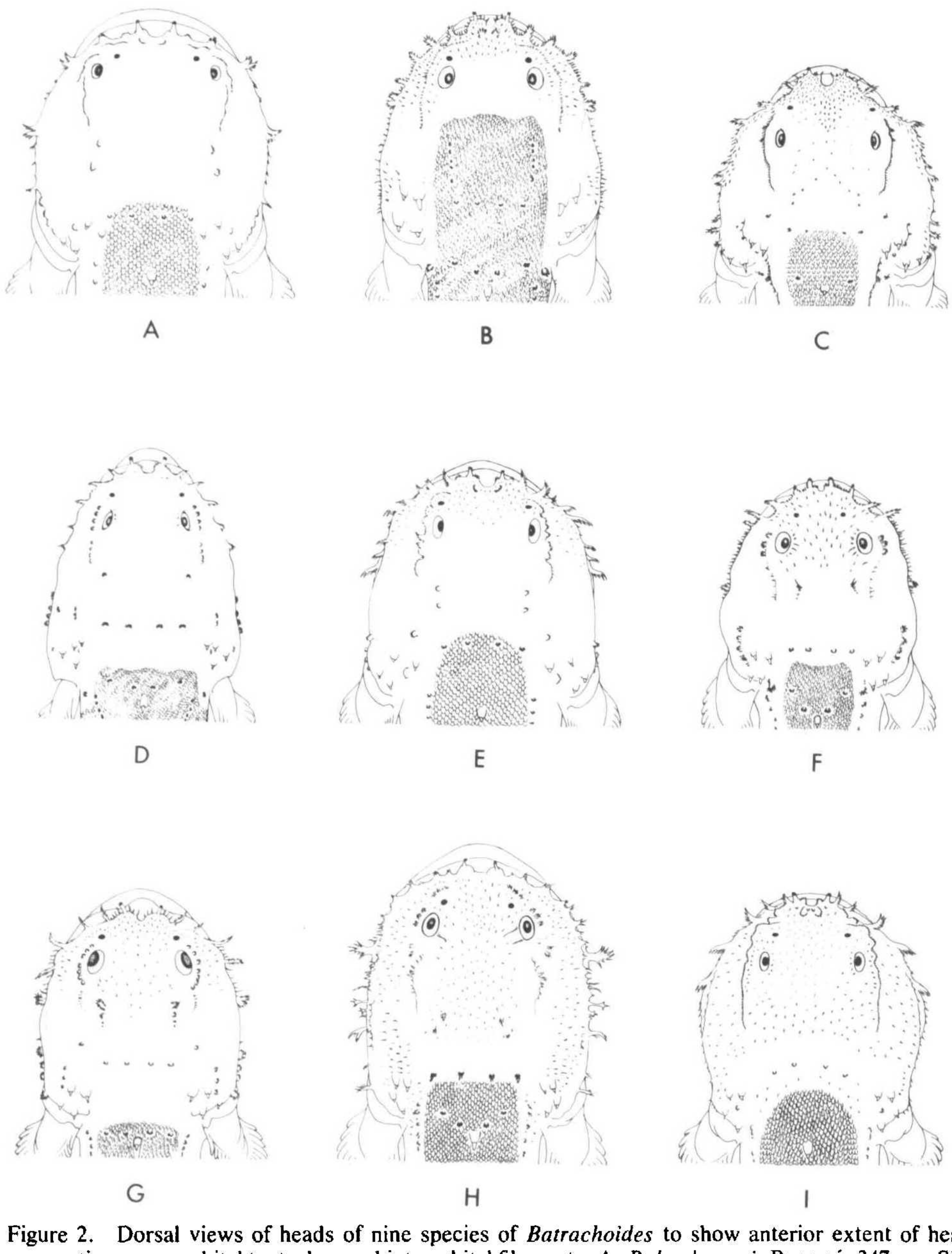

Figure 2. Dorsal views of heads of nine species of *Batrachoides* to show anterior extent of head squamation, supraorbital tentacles, and interorbital filaments. A. *B. boulengeri*, Panamá, 347 mm SL, USNM 80989. B. *B. surinamensis*, N. Brazil, 231 mm SL, USNM 159249. C. *B. waltersi*, Costa Rica, 192 mm SL, LACM 33806-64, holotype. D. *B. walkeri*, Panamá, 170 mm SL, UCLA W53-275, holotype. E. *B. pacifici*, Panamá, 204 mm SL, USNM 80998. F. *B. gilberti*, Panamá, 192 mm SL, USNM 81003, paratype. G. *B. manglae*, Araya Peninsula, Venezuela, 215 mm SL, ANSP 102200. H. *B. goldmani*, Río Usumacinta, 193 mm SL, USNM 219384. I. *B. liberiensis*, Ghana 200 mm SL, USNM uncat.

length 103 mm; head width 83.6 mm; orbit diameter 8.1 mm; interorbital distance 37.4 mm; snout to 2D 128 mm; snout to A 144 mm; P_1 57.1 mm; P_2 39.1 mm. Paratypes CAS SU 12815–6 (2, 280–310); Panamá Bay; C. H. Gilbert and E. C. Starks.

Table 1. Morphometric comparison (as % SL) of *Batrachoides boulengeri*, *B. surinamensis*, *B. waltersi*, and *B. walkeri*

Character	*B. boulengeri* Min.	Max.	x̄	SE	N	*B. surinamensis* Min.	Max.	x̄	SE	N	*B. waltersi* Min.	Max.	x̄	SE	N	*B. walkeri*
Standard Length (mm)	101	352	210.9	20.7	19	97.2	337	198.7	9.7	42	96.2	292	152.7	5.9	54	170
Head Length	33.4	37.2	35.42	0.28	19	27.2	38.6	34.11	0.25	42	34.5	39.3	37.08	0.15	54	33.4
Head Width	25.2	32.3	28.65	0.45	19	21.8	29.9	26.06	0.32	42	25.4	34.3	30.14	0.27	54	25.3
Orbit Diameter	2.5	4.0	3.20	0.10	19	2.0	4.1	3.22	0.07	42	2.9	5.9	4.41	0.07	54	2.8
Interorbital Distance	9.1	14.4	11.46	0.36	19	8.1	12.4	9.58	0.18	42	8.5	12.7	10.34	0.13	54	9.2
Snout–2D	40.8	45.8	43.80	0.30	19	35.0	45.8	43.15	0.29	41	41.0	47.1	44.66	0.19	54	25.1
Snout–A	47.0	55.5	50.90	0.52	19	45.6	54.7	51.01	0.29	41	49.9	58.9	53.00	0.27	53	47.8
Pectoral Length	18.0	23.0	21.03	0.28	19	15.1	23.3	20.15	0.24	42	18.9	23.9	21.28	0.13	53	19.7
Pelvic Length	11.3	15.9	13.56	0.29	19	10.8	21.1	14.01	0.25	42	13.3	17.8	15.63	0.13	54	14.2

Table 2. Number of fin rays in species of *Batrachoides* (Pectoral fin rays counted on left and right sides of holotype of *B. walkeri*)

Species	Dorsal Rays III	21	22	23	24	25	26	27	28	29	30	N	x̄
B. boulengeri	20								2	17		19	28.9
B. surinamensis	103								21	65	4	90	28.8
B. waltersi	81						7	66	7			80	27.0
B. walkeri	1								1			1	28
B. pacifici	84					8	42	3				53	25.9
B. gilberti	33				3	26	9					38	25.2
B. manglae	28	1	11	13	1							26	22.5
B. goldmani	24	1	16	9	2							28	22.4
B. liberiensis	37				1	27	9					37	25.2

Species	Anal Rays 19	20	21	22	23	24	25	26	27	N	x̄	Pectoral Rays 18	19	20	21	22	23	N	x̄
B. boulengeri								16	4	20	26.2				4	7	8	19	22.2
B. surinamensis							6	70	15	91	26.1			9	46	11	1	67	21.1
B. waltersi					3	54	24			81	24.3				3	15	25	43	22.5
B. walkeri							1			1	25		1	1				2	19.5
B. pacifici			3	28	21					52	22.3			8	8	7		23	21.0
B. gilberti				17	21					38	22.6		7	23	2			32	19.8
B. manglae	3	19	4							26	20.0	1	10	8	1			20	19.4
B. goldmani	1	23	4							28	20.1	4	14	11				29	19.2
B. liberiensis			2	15	19					36	22.5		11	15	2			28	19.7

Table 3. Numbers of vertebrae in species of *Batrachoides*

	Precaudal			Caudal										
Species	8	9	10	21	22	23	24	25	26	27	28	29	N	x̄
B. boulengeri			20							2	18		20	27.9
B. surinamensis		1	84							6	67	11	84	28.1
B. waltersi			79					7	59	13			79	26.1
B. walkeri		1									1		1	28
B. pacifici		8	42				3	41	6				50	25.1
B. gilberti		35	2					15	22				37	25.6
B. manglae		26			12	13	1						26	22.6
B. goldmani		19	10	4	16	5	2						27	22.2
B. liberiensis	4	33						14	21				35	25.6

	Total										
	31	32	33	34	35	36	37	38	39	N	x̄
B. boulengeri							2	18		20	37.9
B. surinamensis							6	67	9	82	38.0
B. waltersi					6	60	13			79	36.1
B. walkeri							1			1	37
B. pacifici				11	33	6				50	34.9
B. gilberti				14	22	1				37	34.6
B. manglae	13	13	1							27	31.6
B. goldmani	14	11	2							27	31.6
B. liberiensis			2	14	19					35	34.5

Size and Fecundity.—This is the largest species in the genus, reaching 362 mm SL (GCRL 8402, Panamá Canal Zone, Miraflores Locks). Testes appear to be ripening by 286 mm SL, ovaries by 280 mm. A 303-mm female had 550 eggs, 4.6–5.8 mm in diameter ($\bar{x}$ 5.18); a 352-mm female had 588 eggs, 4.9–6.0 mm ($\bar{x}$ 5.45).

Food Habits.—Five specimens (301–362 mm SL) were examined; food was present in the intestines of 4 (303–362 mm). Three out of four contained crabs, families Xanthidae and Portunidae. One xanthid was *Panopeus chilensis* another possibly *P. purpureus*. Two specimens contained fishes, one of which was a burrfish (Diodontidae, *Chilomycterus*).

Range.—All published records and all known material are from the Bay of Panamá (Fig. 3).

Material Examined.—20 specimens (101–362 mm SL) from 11 collections from the Gulf of Panamá. CAS SU 6487 (1, 286); Panamá Bay; holotype. CAS SU 12815–6 (2, 280–310); Panamá Bay; paratypes. MCZ 12805 (1, 297); Panamá; Albatross. USNM 80989 (1, 347); Panamá City market. USNM 80990–2 (3, 301–352); Canal Zone, Corozal, tidal stream. LACM W53-275-1 (1, 178); between Panamá City and Punta Gorda. LACM W58-304-1 (3, 115–161); between Punta de Hicacal and Río Pasigu. USNM 220127 (4, 101–138); between Río Chico and Punta de la Plata. SIO 64-365 (1, 145); Isla Verde; Inter-Amer. Trop. Tuna Comm., FB 62-66. SIO 69-386 (1, 167) and LACM 31310–1 (1, 165); Gulf of Chiman; 8°42′N, 78°37′W; L. G. Abele 69-58. GCRL 8402 (1, 362); Canal Zone, Miraflores Locks, lower east chamber.

Batrachoides surinamensis (Bloch and Schneider)
Figure 4

Batrachoides tau Lacepède, 1800: 451–454 (original description; western Atlantic; not *Gadus tau* Linnaeus), pl. 12.

Batrachus surinamensis Bloch and Schneider, 1801: 43 (original description; Surinam), pl. 7. Valenciennes in Cuvier and Valenciennes, 1837: 488–494 (description, anatomy, Surinam). Günther,

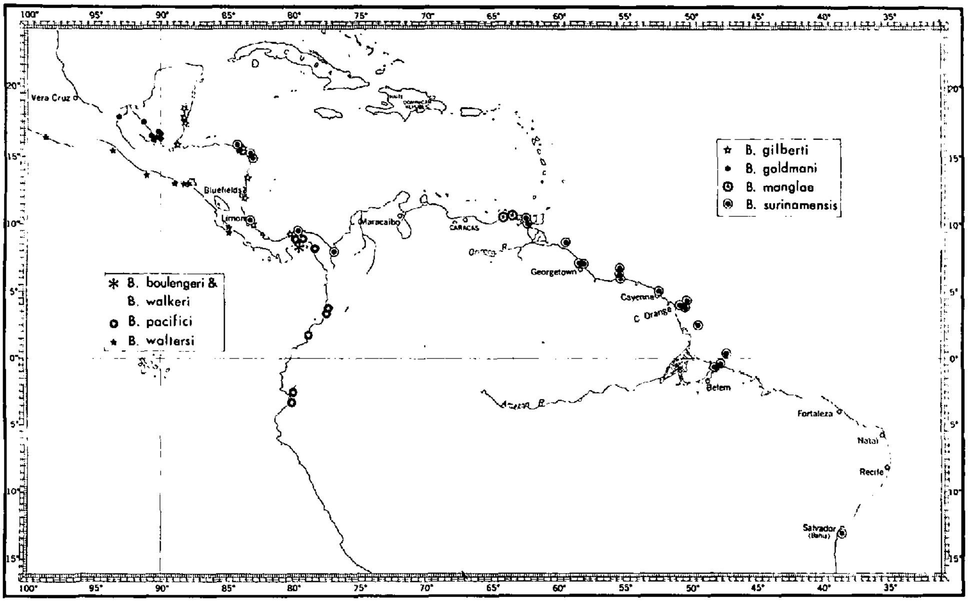

Figure 3. Distributions of the eight American species of *Batrachoides* (based on specimens examined).

1861: 174 (description, in part; Atlantic coast of tropical America only). Boulenger, 1897: 295 (Marajo Is., Brazil). Metzelaar, 1919: 159–160 (2 specimens, from Paramaribo and Georgetown). *Batrachoides surinamensis*. Meek and Hall, 1885: 61 (description; Atlantic coast of tropical America). Jordan and Evermann, 1898: 2314 (description; specimen from Curaçao). Evermann and Goldsborough, 1902: 159 (comparison with *B. goldmani*). Gilbert and Starks, 1904: 183–184 (description and comparison with *B. boulengeri*). Gill, 1907: 402 (Caribbean Sea). Fowler, 1911: 437 (specimen from Pedernales, Venezuela; ANSP 37901, 241 mm SL). Starks, 1913: 71–72 (description; common in Pará market; comparison with *B. pacifici* and *B. boulengeri*). Fowler, 1915: 542 (2 seen, Trinidad). Miranda Ribeiro, 1915: 634–635 (description). Fowler, 1917: 136 (Colon, Panamá Canal Zone, 1 specimen (ANSP 49158), 240 mm SL). Meek and Hildebrand, 1928: 915–916 (synonymy; description based on specimens from Río Truando, Colombia, USNM 9368, 290 mm SL; and Curuca, Brazil, USNM 26646, 130 mm SL). Jordan, Evermann, and Clark, 1930: 486 (listed). Puyo, 1936: 231–234 (description, French Guiana; variety *cayennensis* Puyo). Fowler, 1941: 180 (previous records from Brazil). Fowler, 1944: 473 (listed, in part; Colon; Panamá; Río Truando, Columbia). Puyo, 1949: 254–257 (description, French Guiana, habits, fig. 133). Fowler, 1954: 330 (synonymy; range—Marajó and Pará, Brazil, and Surinam). Röhl, 1959: 496 (description; Venezuela). Lowe, 1962: 677, 696 (British Guiana). Cervigón, 1965: 69 (listed, Venezuela). Cervigón, 1966: 857–858 (description, 5 specimens, Golfo de Paria, Boca Grande del Orinoco). Mago Leccia 1970: 86 (listed; Venezuela). Dahl, 1971: 308–309 (Colombia; to 50 cm long; fig.). Gilbert and Kelso, 1971: 47 (Tortuguero, Costa Rica; UF 12524, 280 mm SL). Roux, 1973: 61 (Brazilian coast). Collette, 1978: Batra 2 (description; range, figs.). Lima and Oliveira, 1978: 9, 17 (common name pacamon in Piauí and Pernambuco states, Brazil, pacamon-preto in Piauí).

Diagnosis.—A large species of *Batrachoides* (maximum size 337 mm SL); with very small eyes (2.0–4.1% SL, $\bar{x}$ 3.22), 2.02–6.21 times in interorbital distance ($\bar{x}$ 3.07); extensive head squamation (to middle of head, Fig. 2B); no supraorbital or interorbital filaments; many lateral line pores (upper (35–51) + (10–25) = 54–68, lower (32–46) + (13–23) = 48–62); many fin rays (dorsal rays 28–29, rarely 30; anal 26–27); moderate numbers of pectoral rays (20–23, usually 21); many vertebrae (usually 10 + 28 = 38); and few pectoral fin glands (usually 3–11, several specimens with none).

Table 4. Numbers of pores in upper and lower lateral lines in species of *Batrachoides* (Data presented by intervals of two pores, means based on original data. Left and right sides of holotype of *B. walkeri* counted)

	Upper Lateral Line																						
Species	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	N	x̄
B. boulengeri													4	2	4	4	2	1				17	56.6
B. surinamensis														6	10	8	18	19	10	6	4	81	61.2
B. waltersi											1	1	4	7	13	19	18	7	—	5		75	58.7
B. walkeri										2												2	46.5
B. pacifici							2	6	14	14	9	6	3									54	46.5
B. gilberti					8	14	8	2	1													33	39.0
B. manglae	1	1	9	8	5	—	1															25	34.1
B. goldmani		1	10	2	1	5	4															23	35.3
B. liberiensis		1	—	5	7	9	7	1														30	37.6

	Lower Lateral Line																						
	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	N	x̄
B. boulengeri												1	6	3	6	2	1						19	50.9
B. surinamensis													1	3	2	9	6	19	20	9	7	1	77	58.9
B. waltersi											1	2	7	16	15	9	11	4	—	1			66	52.8
B. walkeri									1	—	—	1											2	43.5
B. pacifici							2	9	13	10	16	3											53	41.9
B. gilberti					1	8	8	12	3														32	36.9
B. manglae	2	1	2	9	10	2																	26	31.0
B. goldmani			5	7	6																		18	30.6
B. liberiensis						1	10	12	5	1													29	38.0

Table 5. Numbers of pectoral fin glands in species of *Batrachoides* (Left and right sides of holotype of *B. walkeri* counted)

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	N	x̄
B. boulengeri																	3	6	10	1	20	17.4
B. surinamensis	6	—	—	2	6	7	12	14	20	22	10	3									102	7.1
B. waltersi															3	3	20	51	54	6	137	17.2
B. walkeri								1	1												2	7.5
B. pacifici											1	8	27	31	23	2	4				96	12.9
B. gilberti	7	3	1	3	1	7	5	2	1												30	3.5
B. manglae					1	—	4	3	6	8	2	3									27	8.2
B. goldmani														3	10	6	3	1			23	14.5
B. liberiensis														7	17	9	1				34	14.1

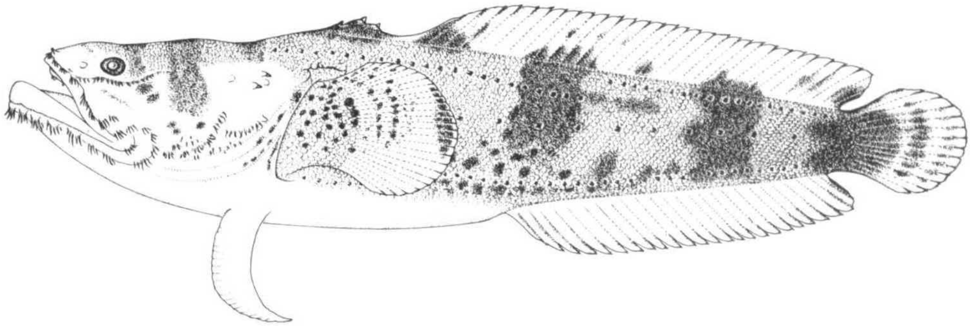

Figure 4. *Batrachoides surinamensis,* USNM 219454, 310 mm SL, French Guiana, Cayenne market, drawn by Keiko Hiratsuka Moore.

Body proportions are presented in Table 1, counts in Tables 2–5. Teeth on dentary 21–27 (31), premaxilla (27) 34–43, palatine 13–18, and vomer 8–19, usually 10–14.

Very similar to *B. boulengeri* in large body size, small eye size, and high counts of most meristic characters but differs sharply in having many fewer pectoral fin glands (0–11 vs. 16–19) and in having a much more extensive head squamation (reaching anteriorly to middle of head instead of just to supratemporal canal). Differs from the two other Atlantic species with which it may co-occur (*B. manglae* and *B. gilberti*) in having more dorsal and anal fin rays and vertebrae and a much smaller eye.

Types.—We do not know if there are any extant type-specimens for *Batrachoides tau* Lacepède or *Batrachus surinamensis* Bloch and Schneider.

Size and Fecundity.—This is the second largest species in the genus, reaching 337 mm SL (MCZ 12776, Brazil, Maranhao). Testes appear to be about ripe by 245 mm SL, ovaries by 211 mm. A 211-mm female from Guyana had 432 eggs, 4.3–5.9 mm in diameter ($\bar{x}$ 5.10); a 225-mm female from Honduras had 451 eggs, 3.2–4.7 mm ($\bar{x}$ 4.03).

Food Habits.—Ten specimens (133–293 mm SL) were examined, 9 contained food items. Crabs were present in 6 of 9. Five families were represented: Calappidae (*Hepatus scaber*), Portunidae (*Cronius ruber* in one case), Xanthidae, Pinnotheridae, and Palicidae (*Palicus*). Shrimps were also present in 6 of 9 guts. Three families were found: Penaeidae, Palaemonidae (almost certainly *Brachycarpus biunguiculatus*), and Alphaeidae. A stomatopod was present in one gut and there were fish bones in another.

Range.—Widespread along the Caribbean and Atlantic coasts of Central and South America from Honduras to Salvador (Bahia) Brazil (Fig. 3). Previously known only as far north as Colon, Panamá Canal Zone (Fowler, 1917, 1944) and Tortuguero, Costa Rica (Gilbert and Kelso, 1971). D. W. and T. A. Greenfield and R. K. Johnson took several specimens in Brus Lagoon, Honduras on the M/V SABRINA in May 1975 and several more were taken along the coast of Honduras from Caratasca to Río Cruta by the M/V SHADY LADY in April 1967 (see material examined). The record of *B. surinamensis* from Trinidad (Caldwell and Caldwell, 1964:40) is based on a mis-identified specimen of *Amphichthys* (LACM 22137). At the southern end of the range, most published records (Boulenger, 1897;

Starks, 1913; Meek and Hildebrand, 1928) and most collections (R/V OREGON I and II; Thayer Expedition) are from around the mouth of the Amazon River (Marajo I., Pará, Curucá, Vigia). The known southern limit of the range is presently Salvador (MCZ Thayer Expedition specimens from Bahia).

Geographic Variation.—To see if geographic variation was present in *B. surinamensis,* our study material was divided into seven samples from Honduras to Salvador, Brazil. Inspection of the frequency distributions indicated that much geographic variation was present in three characters: number of pores in the upper and lower lateral lines and number of pectoral fin glands (Table 7). In order to determine if the variation was statistically significant, the seven samples were combined into four samples: Honduras, Central America (from Costa Rica to Colombia), northern South America (Venezuela, the Guianas, and Brazil north of the equator), and "southern" South America (Brazil south of the equator).

The number of upper lateral line pores ranged from 54 to 68. Sample sizes and means were: Honduras ($n = 9$, $\bar{x} = 59.0$ pores), Central America ($n = 21$, $\bar{x} = 63.2$), northern South America ($n = 38$, $\bar{x} = 62.2$), southern South America ($n = 13$, $\bar{x} = 56.3$). The ANOVA procedure rejected the hypothesis that all four means were equal ($P = 4.5 \times 10^{-6}$). In order to determine which mean or means were different, the Newman-Keuls procedure was used. At the .05 level of significance, samples from Central America and northern South America are not significantly different with respect to mean number of upper lateral line pores; samples from southern Brazil and from Honduras are significantly different from each other and from the northern South America and Central America samples.

The number of lower lateral line pores ranged from 49 to 66. Sample sizes and means were: Honduras ($n = 9$, $\bar{x} = 55.9$ pores), Central America ($n = 22$, $\bar{x} = 60.5$), northern South America ($n = 35$, $\bar{x} = 59.3$), southern South America ($n = 9$, $\bar{x} = 54.9$). The ANOVA procedure rejected the hypothesis that all four means were equal ($P = 6.1 \times 10^{-6}$). From the MRT procedure we determined that the samples from Honduras and southern South America do not have significantly different means and that the samples from Central America and northern South America do not have significantly different means. However, the Honduras and southern South America samples, are significantly different from the Central America and northern South America samples.

The number of pectoral fin glands ranged from 0 to 11. Sample sizes and means were: Honduras ($n = 13$, $\bar{x} = 8.8$ glands), Central America ($n = 21$, $\bar{x} = 5.9$), northern South America ($n = 43$, $\bar{x} = 8.5$), southern South America ($n = 25$, $\bar{x} = 4.9$). The ANOVA procedure rejected the hypothesis that all four means were equal ($P = 2.6 \times 10^{-11}$). From the MRT procedure we determined that the samples from southern South America and Central America are not significantly different and that the populations from northern South America and Honduras are not significantly different. However the populations from southern South America and Central America are significantly different from the populations from northern South America and Honduras.

Morphometric data from three geographic samples of *B. surinamensis* were submitted to ANCOVA testing: Honduras (13 specimens, 102–260 mm SL, $\bar{x} = 156.4$); French Guiana (17 specimens, 97.2–337, $\bar{x} = 233.0$); and Salvador, Brazil (8 specimens, 120–214, $\bar{x} = 171.0$). No differences in regressions were detected at the .05 level of significance for 8 of the nine dependent variables. However, the ANCOVA procedure did detect a difference in the length of the pelvic fins of the three geographic samples. The hypothesis that the slopes of all three regressions are equal was accepted ($P = 0.47$), but the hypothesis that the Y intercepts of the three populations are equal was rejected ($P = 0.0079$). The sample of *B.*

surinamensis from Salvador had the shortest pelvic fin with respect to standard length, a = −3.06 mm, the sample from French Guiana was intermediate, a = −1.36 mm, and the sample from Honduras had the largest pelvic fin relative to standard length, a = 1.38 mm. These data were submitted to the MRT procedure but this procedure was unable to determine which Y intercepts were different from others.

Material Examined.—115 specimens (17.3–337 mm SL) from 53 collections.

HONDURAS. 16 (17.3–260) from 8 collections. USNM 44463 (1, 208); Patuca. FMNH 84547 (1, 17.3); Brus Lagoon; M/V SABRINA 75-27. FMNH 84548 (1, 149); Brus Lagoon; M/V SABRINA 75-26. FMNH 84549 (1, 260); Brus Lagoon; M/V SABRINA 75-30. UF 23108 (2, 108–110); Caratasca to Río Cruta; 15°19′N, 83°26′W; SHADY LADY Un6703. UF TABL 104838 (3, 132–176); Caratasca to Río Cruta; 15°21′N, 83°34′W; SHADY LADY Un6703. UF TABL 104839 (6, 102–134); off Río Cruta; 15°18′N, 83°22′W; SHADY LADY Un6703. UF TABL 104840 (1, 225); off Río Cruta; 15°26′N, 83°41′W; SHADY LADY Un6703.

COSTA RICA. 1 (280) from 1 collection. UF 12524 (1, 280); Limon Prov., Tortuguero Lagoon.

PANAMÁ. 19 (47.8–240) from 2 collections. ANSP 49158 (1, 240); Canal Zone, Colon. GCRL V72:8688 (19, 48.2–89.6); Colon, Gatun Locks, lower W chamber.

COLOMBIA. 1 (290) from 1 collection. USNM 9368 (1, 290); Río Truando.

VENEZUELA. 2 (134–241) from 2 collections. ANSP 37901 (1, 241); Pedernales, near mouth of Orinoco R. UF 11618 (1, 134); 10°29′N, 62°21′W; 8 fms; R/V OREGON 4494.

GUYANA. 8 (173–276) from 5 collections. FMNH 59459 (1, 193); Georgetown market. MCZ 30164 (1, 250); Georgetown market. CAS IU 11782-3 (2, 248–276); Georgetown market. AMNH 9319 (2, 173–213); and 18580 (1, 190); Demerara River. UF TABL 104319 (1, 211); 8°45′N, 59°15′W; M/V CALAMAR 67-10.

SURINAM-FRENCH GUIANA. 15 (74.4–311) from 8 collections. FMNH 66853 (1, 137); 5°31′N, 53°0′W; 19 fms; R/V OREGON 2037. FMNH 66854 (3, 162–188); 5°46′N, 53°0′W; 15 fms; R/V OREGON I 2038. FMNH 88024 (3, 74.4–142); 15 fms; M/V COQUETTE. FMNH 89581 (1, 213); 25–30 fms; M/V COQUETTE. USNM 219454 (3, 270–311); Cayenne market; B. B. Collette 1575. USNM 219570 (1, 240); 6°23′N, 54°50′W; 13 fms; R/V OREGON II 10597. USNM 219568 (2, 260–281); 6°28′N, 54°51′W; 16 fms; R/V OREGON II 10601. USNM 219569 (1, 241); 6°25′N, 54°59′W; 17 fms; M/V COQUETTE 6.

BRAZIL. 54 specimens (52.1–337 mm SL) from 27 collections. USNM 159249 (3, 204–231); N. Brazil-French Guiana; R/V OREGON. USNM 219457 (2, 242–293); 4°48′N, 51°19′W; 32 fms; R/V OREGON II 17628. USNM 219455 (2, 207–237); 4°14′N, 50°36′W; 38–43 fms; R/V OREGON II 17644. USNM 159235 (1, 232); 4°02′N, 50°35′W; 38 fms; R/V OREGON I 2049. USNM 219456 (2, 111–198); 3°55′N, 50°34′W; 30 fms; R/V OREGON II 17648. USNM 219458 (2, 177–235); 3°50′N, 50°15′W; 32 fms; R/V OREGON II 17650. USNM 219460 (1, 103); 3°37′N, 50°33′W; 19 fms; R/V OREGON II 17656. USNM 184852 (1, 97.2); 2°34′N, 49°18′W; 10 fms; R/V OREGON I 2055. USNM 219459 (2, 97.3–274); 2°05′N, 48°35′W; 10 fms; R/V OREGON II 17684. USNM uncat. (1, 205); 2°05′N, 48°14′W; 25 fms; R/V OREGON II 17686. USNM 219463 (4, 133–178); 1°26′N, 48°14′W; 16 fms; R/V OREGON II 17694. USNM 219461 (2, 181–191); 1°03′N, 47°49′W; 26 fms; R/V OREGON II 17710. USNM 219462 (3, 96.5–265); 0°48′N, 47°45′W; 25–26 fms; R/V OREGON II 17712. FMNH 66274 (1, 177); 0°27′S, 47°09′W; R/V OREGON I 4215. MCZ 4630 (1, 310), MCZ 50086 (2, 107–234), MCZ 12770 (3, 52.1–253), and USNM 26646 (1, 130); Curucá; Thayer Expedition. MCZ 12777 (2, 107–122); Pará; Thayer Expedition. MCZ 12771 (1, 91.8); Vigia; Thayer Expedition. MCZ 12776 (2, 208–337); Maranhao; Thayer Expedition. CAS SU 22149 (4, 148–309); Pará market; Stanford Expedition. CAS SU 30873 (1, 96.0); Curucá; IU 2080. FMNH 87012 (1, 207); Río Caete mouth; Haseman No. 3374. FMNH 92074 (1, 158); Pará; Haseman No. 3443. MCZ 12773 (4, 120–189) and MCZ 12774 (4, 173–214); Bahia; Thayer Expedition.

Batrachoides waltersi new species
Figure 5

Batrachoides pacifici, not of Günther. Ramírez H. and González P., 1976: 130 (in key, range in part, Acupulco south to but not including Panamá).

Diagnosis.—A medium-sized species of *Batrachoides* (maximum size 292 mm SL); with small eyes (2.9–5.9% SL, $\bar{x}$ 4.41), 1.45–4.12 times in interorbital distance ($\bar{x}$ 2.38); many lateral line pores (upper (39–54) + (6–17) = 48–67; lower (31–42) + (10–19) = 44–62); many fin rays (dorsal rays 26–28, usually 27; anal rays 23–25, usually 24–25); many vertebrae (usually 10 + 26 = 36); and many pectoral fin glands (14–19, usually 16–18).

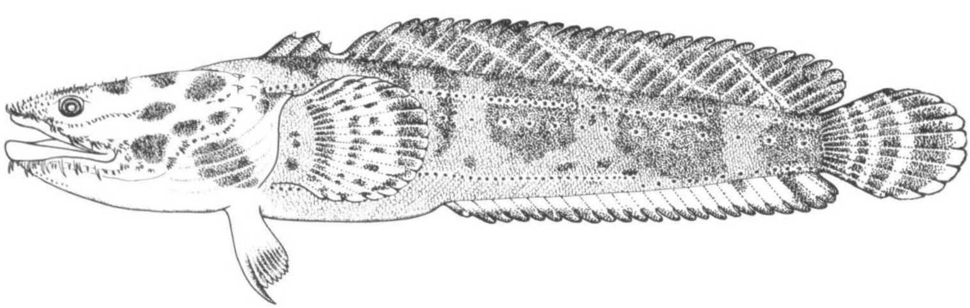

Figure 5. *Batrachoides waltersi* Collette and Russo, n. sp., holotype, LACM 33806-64, 192 mm SL, Costa Rica, Golfo de Nicoya, drawn by Keiko Hiratsuka Moore.

Body proportions are presented in Table 1, counts in Tables 2–5. Teeth on dentary 17–23, premaxilla 32–40, palatine 10–15, and vomer 5–10.

Most similar to *B. boulengeri* and *B. surinamensis* in large body size and high counts of lateral line pores. Fewer fin rays (dorsal rays 26–28, usually 27 vs. 28–30; anal rays 23–25, usually 24 or 25 vs. 26 or 27) and vertebrae (total 35–37, usually 36 vs. 37–39, usually 38) than in those two species. Resembles *B. boulengeri* and sharply differs from *B. surinamensis* and *B. walkeri* in having many pectoral fin glands (14–19 vs. 0–11, Table 5).

Types.—Holotype LACM 33806-64 (immature female, 192); Costa Rica, Puntarenas, WSW of Boca Burrance; C. Swift; 12 June 1973; D III, 28; A 24; P_1 23–23; vertebrae 10 + 27 = 37; upper lateral line 51 + 8 = 59; lower lateral line 41 + 12 = 53; P_1 glands 18–18; head squamation extending anterior as far as supratemporal canal (Fig. 2C); no supraorbital tentacles; interorbital filaments concentrated on snout but several filaments scattered on the other parts of the dorsal surface of the head (Fig. 2C); head length 70.6 mm; head width 62.3 mm; orbit diameter 7.0 mm; interorbital distance 22.1 mm; snout–2D 78.8 mm; snout–A 104 mm; P_1 41.2 mm; P_2 30.5 mm. Paratypes: the other 141 specimens (28.5–292 mm) listed under material examined.

Etymology.—Named for Vladimir Walters, colleague and student of toadfishes who recognized the distinctness of this species a number of years ago.

Size and Fecundity.—A medium-sized species, reaching 292 mm SL (USNM 219786, El Salvador, Jiquilisco Bay). Testes appeared to be ripening by 183 mm SL, ovaries by 154 mm. A 202-mm female from the Gulf of Tehuantepec had 182 eggs, 5.5–7.0 mm in diameter ($\bar{x}$ 6.10).

Food Habits.—Six specimens (151–226 mm SL) were examined; the stomach and intestine of the 226 mm specimen were empty. All 5 specimens with food contained crabs. Four families were represented: Paguridae, Leucosiidae (*Persephona*, probably *P. townsendi*), Xanthidae, and Pinnotheridae (*Pinnotheres*). Gastropod shells were present in 3 of 5 but these were hermit crab homes in at least one case. Many fish bones were present in one specimen.

Range.—Eastern tropical Pacific from the mouth of Río Dulce, México (16°29′N, 98°45′W) south to the Gulf of Nicoya, Costa Rica (Fig. 3). Probably extending north at least as far as Acapulco if the record of *B. pacifici* reported by Ramírez and González (1976) was based on material of *B. waltersi*.

Geographic Variation.—In order to determine if a significant amount of geographic variation exists in the number of pores in the upper lateral line of *B. waltersi*, our material was grouped into three populations: Gulf of Tehuantepec (n = 29, $\bar{x}$ = 59.2 pores), Guatemala-El Salvador (n = 29, $\bar{x}$ = 59.2), and Costa Rica (n = 17, $\bar{x}$ = 55.6 pores). The analysis of variance procedure rejected the null hypothesis that all three means are equal (P = .00019). In order to determine which mean or means are different, the Newman-Keuls procedure was used. From this we conclude (at the .05 level of significance) that the mean numbers of upper lateral line pores are equal for the Gulf of Tehuantepec and the El Salvador populations and both of these are different from the Costa Rica population.

Similar results were obtained when we compared number of pores in the lower lateral line of *B. waltersi*. The material was grouped into the same three samples: Gulf of Tehuantepec (n = 26, $\bar{x}$ = 54.0), Guatemala-El Salvador (n = 25, $\bar{x}$ = 53.1), and Costa Rica (n = 15, $\bar{x}$ = 50.1). The analysis of variance procedure rejected the null hypothesis that all three means are equal (P = .00081). From the Newman-Keuls procedure we conclude (α .05) that the mean numbers of lower lateral line pores are equal for the Gulf of Tehuantepec and the El Salvador populations and both of these are different from the Costa Rica population.

Morphometric data from three geographic samples of *B. waltersi* were tested with the ANCOVA procedure: Gulf of Tehuantepec (17 specimens; 104–201 mm SL, $\bar{x}$ = 130.8); El Salvador (19 specimens; 97.8–292, $\bar{x}$ = 168.6), and Costa Rica (18 specimens; 96.2–245, $\bar{x}$ = 156.6). No differences in regressions were detected at the .05 level of significance for eight of the nine dependent variables. However, the ANCOVA procedure did detect a difference in the head length among the three geographic samples. The hypothesis that the slopes are equal was accepted (P = .06), but the hypothesis that the Y intercepts of all three regressions are equal was rejected (P = .007). The sample of *B. waltersi* from El Salvador has the lowest intercept (a = −4.06), the sample from Costa Rica is intermediate (a = −2.02) and the sample from the Gulf of Tehuantepec is the highest (a = 1.85). To determine which intercepts are different from others, these data were submitted to the MRT procedure. The hypothesis that all three intercepts are equal was accepted (.5 > P > .2). The MRT procedure was unable to determine which populations were different from others.

Material Examined.—142 specimens (25.0–292 mm SL) from 33 collections.

MÉXICO. 31 specimens (28.5–201 mm SL) from 3 collections. CAS SU 57002 (1, 28.5); mouth of Río Dulce; 16°29′N, 98°45′W; M/V ZACA sta. 191 D-1. SIO 63-517 (11, 35.3–201); Gulf of Tehuantapec; 14°45′N, 92°35′W; 9–10 fms. SIO 73-257 (19, 95.1–146); NE shore Gulf of Tehuantapec; 15°30′N, 93°22′W; 12–12.5 fms; R/V ALEXANDER AGASSIZ.

GUATEMALA. GCRL V72:9340 (4, 61.2–114); off central coast; 55–73 m.

EL SALVADOR. 86 specimens (25.0–292 mm SL) from 19 collections. LACM W70-5-1 (3, 129–183); Golfo de Fonseca, Chirquiri Bay; R/V TE VEGA. SIO 73-276 (11, 50.3–245); Golfo de Fonseca, SW of Punta Amapela; 13°5.1–6.5′N, 87°57.6–59.5′W; 13–16 fms; R/V ALEXANDER AGASSIZ. UA 68–77 (1, 152); Golfo de Fonseca, Punta Chiquirín; 13°17.1′N, 87°47.4′W.

The following 71 specimens were taken by P. C. Phillips at 6 stations in Jiquilisco Bay in 1976. USNM 219788 (3, 163–226); Punta San Juan; 4 Feb. USNM 219787 (1, 234); Punta San Juan; 8 Sept. USNM 219789 (2, 50–55); La Caramba; 27 Jan. FMNH 91905 (3, 94–127); La Venadona; 24 Feb. BMNH 1979.4.5.1–2 (2, 96–106); La Venadona; 16 March. WAM P-2649-001 (2, 72–84); La Venadona; 7 Sept. USNM 219790 (7, 25–94); Los Lagartos; 10 Feb. USNM 219791 (3, 61–182); Río Chaguantique; 21 Jan. USNM 219792 (11, 83–106); Río Chaguantique; 11 Feb. CAS 42798 (3, 113–188); Río Chaguantique; 14 Sept. USNM 219794 (8, 53–95); El Potrero; 28 Jan. MNHN 1979-280 (1, 84); El Potrero; 18 Feb. MCZ 54337 (2, 100); El Potrero; 10 March. ANSP 140787 (3, 68–94); El Potrero; 14 July. USNM 219793 (5, 84–92); El Potrero; 1 Sept. USNM 219786 (15, 41–292); Jiquilisco Bay; Sept. 1975–March 1976.

NICARAGUA. UCR 360-34 (1, 194); 1–12 mi W of mouth of Golfo de Fonseca.

COSTA RICA. 20 specimens (74.0–245 mm SL) from 9 collections. USNM 94613 (1, 178); Golfo de

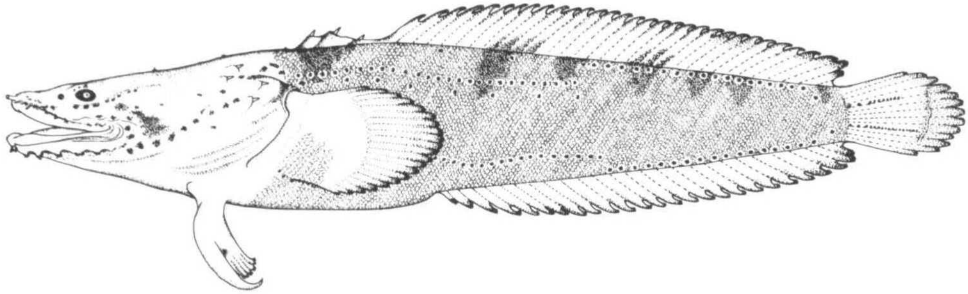

Figure 6. *Batrachoides walkeri* Collette and Russo, n. sp., holotype, USNM 220128, 170 mm SL, ripe female, Panamá Bay, drawn by Keiko Hiratsuka Moore.

Nicoya. USNM 220129 (2, 128–183); Golfo de Nicoya; Chira flats. LACM W54-434-1 (1, 203); Costa Rica. LACM 30745-3 (5, 121–245); LACM 30715-17 (1, 221); LACM 9754-29 (1, 117); LACM 30728-5 (1, 96.2); and LACM 33806-64 (6, 74.0–192); Golfo de Nicoya, Puntarenas. UCR 297-31 (2, 86.5–116); Golfo de Nicoya.

Batrachoides walkeri new species
Figure 6

Diagnosis.—A small species of *Batrachoides* (size of only known specimen, a ripe female, 170 mm SL); with very small eyes (2.8% SL), 3.27 times in interorbital width; reduced head squamation (scales extending about half way from dorsal fin origin to supratemporal canal, Fig. 2D); 2–3 short stubby filaments above each eye; no interorbital filaments; a moderate number of lateral line pores (upper 27 + 19 = 46, lower 29 + 17 = 46); many dorsal (28) and anal (25) fin rays; a moderate number of pectoral fin rays (19 or 20); many vertebrae (9 + 28 = 37); and a moderate number of pectoral fin glands (7 or 8).

Body proportions are presented in Table 1, counts in Tables 2–5. Teeth on dentary 26–28, premaxilla 36–38, palatine 15–20, and vomer 17.

Generally similar to *B. boulengeri* and *B. surinamensis* in small eye size and high vertebral and dorsal ray counts but differing sharply from *B. boulengeri* by having only 7 or 8 pectoral fin glands (vs. 16–19) and only 19 or 20 pectoral fin rays (vs. 21–23) and from both *B. boulengeri* and *B. surinamensis* in having scales extending only about half way from the origin of the dorsal fin to the supratemporal canal (instead of slightly past the supratemporal canal in *B. boulengeri* and to the middle of the head in *B. surinamensis*). Most similar to *B. pacifici* in interorbital width (9.2% SL) and number of pores in the upper lateral line (46 vs. 40–52) but at one extreme or the other of the range in number of pores in the lower lateral line (46) for *B. pacifici* (36–46) and the three species with high counts, *B. boulengeri, B. waltersi,* and *B. surinamensis* (47 or 48 to 56–62).

Types.—Holotype (and only known specimen) USNM 220128 (ripe female, 170); Panamá Bay between Panamá City and Punta Gorda; R. Rosenblatt; 1–5 July 1953; D III, 28; A 25; P_1 20–19; vertebrae 9 + 28 = 37; upper lateral line pores 27 + 19 = 46; lower lateral line 29 + 17 = 46; P_1 glands 8–7; head squamation extending forward half way between dorsal fin origin and supratemporal canal (Fig. 2D); 2–3 short stubby tentacles over each eye; no interorbital filaments; head length 56.8 mm; head width 43.0 mm; orbit diameter 4.8 mm; interorbital distance 15.7 mm; snout to 2D 72.7 mm; snout to A 81.3 mm; P_1 33.5 mm; P_2 24.2 mm.

Table 6. Geographic variation in lateral line pores and pectoral fin glands in *Batrachoides surinamensis*

	Upper Laterial Line Pores																
Area	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	N	x̄
Honduras		2	1	1	–	–	1	2	1	–	1					9	59.00
Costa Rica-Colombia						1	1	4	4	5	–	–	2	2	2	21	63.24
Venezuela-Guyana						1	2	–	1	–	1	–	–	1	1	7	62.86
Surinam-French Guiana					1	–	1	1	–	1	–	2				6	62.00
N. Brazil				1	3	1	1	4	5	2	1	5	1	–	1	25	62.12
Amazonian Brazil		1	3	1	–	–	1									6	56.67
Salvador, Brazil	1	2	2	1	–	1										7	56.00

	Lower Lateral Line Pores																		
	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	N	x̄
Honduras		1	–	–	1	1	2	1	–	1	–	–	2						9	55.89
Costa Rica-Colombia							1	–	1	–	4	2	4	2	1	4	3		22	61.36
Venezuela-Guyana					1	–	–	–	–	1	1	3	2						8	59.00
Surinam-French Guiana							1	–	1	–	1	1	–	1	1				6	59.33
N. Brazil						1	2	1	1	5	3	3	2	3	1	–	–	1	23	59.17
Amazonian Brazil		1	–	–	–	1	–	–	–	2	–	1							5	56.00
Salvador, Brazil	1	–	1	–	–	–	–	1	–	1									4	53.50

	Pectoral Fin Glands													
	0	1	2	3	4	5	6	7	8	9	10	11	N	x̄
Honduras							2	–	3	4	1	3	13	8.8
Costa Rica-Colombia					4	4	6	5	2				21	5.9
Venezuela-Guyana									2	1	1		4	8.8
Surinam-French Guiana								3	4	5	2		14	8.4
N. Brazil				1	–	–	1	2	6	9	6		25	8.5
Amazonian Brazil	3	–	–	–	1	2	2	4	2	3			17	5.7
Salvador, Brazil	3	–	–	1	1	1	1	–	1				8	3.3

Table 7. Morphometric comparison (as % SL) of *Batrachoides pacifici* and *B. gilberti*

Character	*B. pacifici*					*B. gilberti*				
	Min.	Max.	x̄	SE	N	Min.	Max.	x̄	SE	N
Standard Length (mm)	83.7	286	184.5	13.2	22	60.9	230	147.1	11.3	23
Head Length	35.1	38.8	37.06	0.21	22	36.4	40.4	38.13	0.21	23
Head width	26.8	33.7	30.46	0.37	22	25.6	34.4	28.46	0.46	23
Orbit Diameter	4.3	7.1	5.83	0.17	22	4.0	6.9	5.35	0.20	23
Interorbital Distance	5.9	11.5	8.85	0.39	21	5.7	10.3	8.36	0.30	23
Snout-2D	42.7	48.2	45.70	0.32	22	44.7	49.6	47.45	0.25	23
Snout-A	49.3	58.7	54.44	0.51	22	51.2	56.7	53.88	0.35	23
Pectoral Length	17.9	23.7	20.39	0.30	22	19.6	24.8	21.90	0.26	23
Pelvic Length	13.1	18.2	14.90	0.23	22	13.0	16.9	15.43	0.18	23

Etymology.—Named for Boyd W. Walker, professor of Ichthyology at the University of California at Los Angeles and long-term student of eastern Pacific fishes, who first recognized that the type might represent an undescribed species and who made available to us the toadfish collections at UCLA.

Size and Fecundity.—Apparently a small species, known only from the 170 mm ripe female. It has 172 eggs, 3.8–4.1 mm in diameter (x̄ 3.69).

Range.—The only known specimen is from Panamá Bay (Fig. 3) where it was taken with a specimen of *B. boulengeri.*

Batrachoides pacifici (Günther)

Batrachus pacifici Günther, 1861: 173–174 (original description; Pacific coast of Panamá; 2 specimens, 96.7–162 mm SL, BMNH 1860.6.16.222 & 18.11). Günther, 1869: 435 (*B. liberiensis* Steindachner may be a synonym). Steindachner, 1879: 160 (Mamoni R. at Chepo, Panamá).

Batrachoides pacifici. Gill, 1864: 170. Jordan and Gilbert, 1883a: 111 (Panamá; USNM 29267, 29306, 29349, 29473). Jordan and Gilbert, 1883b: 626 (Panamá; listed). Meek and Hall, 1885: 62 (synonymy; 1 specimen from Panamá). Steindachner, 1902: 123 (pigmentation; 203 mm specimen from Guayaquil). Jordan and Evermann, 1898: 2314–5 (description; Panamá). Gilbert and Starks, 1904: 181–2 (description; very abundant at Panamá, adults in the markets, young in tide-pools). Gill, 1907: 402 (coast of Panamá). Kendall and Radcliffe, 1912: 159 (Panamá Bay). Fowler, 1916: 412 (Panamá). Eigenmann, 1922: 217 (Guayaquil, Ecuador; listed after Steindachner). Meek and Hildebrand, 1928: 912–913 (description; Panamá; 32 specimens, 28–340 mm). Jordan, Evermann, and Clark, 1930: 487 (listed). Fowler, 1944: 181 (description; synonymy; Balboa Harbor, Panamá; 1 specimen, 292 mm), 415 (fig. 256), 525 (listed; Ecuador and Panamá). Chirichigno, 1976: 70–71 (description; Peru; 2 specimens, 120–132 mm SL; fig. 24). Ramírez H. and González P., 1976: 130 (in key, range in part, only Panamá).

Diagnosis.—A medium-sized species of *Batrachoides* (maximum size 286 mm SL); with large eyes (4.3–7.2% SL, x̄ 5.83), 0.82–2.62 times in interorbital distance (x̄ 1.58); moderate head squamation (extending just anterior to supratemporal canal, Fig. 2E); a moderate number of lateral line pores (upper (25–36) + (11–21) = 40–52, lower (23–33) + (10–16) = 36–46); a moderate number of fin rays (dorsal rays 25–27, usually 26; anal rays 21–23, usually 22–23); a moderate number of vertebrae (usually 10 + 25 = 35); and a moderately high number of pectoral fin glands (10–16).

Body proportions are presented in Table 7, counts in Tables 2–5. Teeth on dentary 14–19 (21), premaxilla 23–31, palatine 10–14, and vomer 6–8 (12).

Most similar to the western Atlantic *B. gilberti* in body size, eye size (Table 7), head squamation (Fig. 2E) and most meristic characters but differs sharply in having more pectoral fin glands (10–16 vs. 0–8, Table 5). Also, has fewer teeth

on the dentary, premaxilla, palatine, and vomer. Differs from *B. boulengeri* and *B. walkeri* which both are also found in the Bay of Panamá in having fewer dorsal and anal fin rays (Table 2). Has fewer pectoral fin glands than *B. boulengeri* (10–16 vs. 16–19) but more than *B. walkeri* (7–8).

Types.—Lectotype, herein designated, BMNH 1860.6.18.11 (1, 164); Panamá Coast; Mr. Fraser's collection; D III, 26; A 22; P_1 22; vertebrae 10 + 25 = 35; upper lateral line 30 + 17 = 47; P_1 glands 14–14; head squamation extending forward just short of supratemporal canal; no supraorbital filaments; small patch of filaments anterior to interorbital area; head length 57.0 mm; head width 48.0 mm; orbit diameter 10.1 mm; interorbital distance 12.4 mm; snout to 2D 72.5 mm; snout to A 86.5 mm; P_1 32.7 mm; P_2 26.3 mm. Paralectotype BMNH 1860.6.16.222 (1, 96.7), same collection data as lectotype.

Size and Fecundity.—This is the largest of the three medium-sized species of *Batrachoides,* reaching 286 mm SL (USNM 80997, Panamá City). Males showed ripening testes by 214 mm SL, a 204-mm female from Colombia appeared ripe. The 204-mm female had 202 eggs, 3.5–5.0 mm in diameter ($\bar{x}$ 4.42).

Food Habits.—Five specimens (119–244 mm SL) were examined; all contained crabs. Xanthid crabs were present in 4 of 5, identifiable to *Panopeus* (almost certainly *P. purpureus*) in one case. Porcellanid crabs were present in 3 of 5, identifiable to *Petrolisthes* in two cases. Possible fragments of a grapsid crab were also found in a specimen from Miraflores Locks.

Range.—Found from the Canal Zone in Panamá (Fig. 3) south to northern Peru (Tumbes, GCRL 12555; Puerto Pizzaro and Punta Malpelo, Chirichigno, 1976). Sometimes enters freshwater (Mamomi River, Chepo, Panamá; Steindachner, 1879).

Material Examined.—164 specimens (22.2–286 mm SL) from 56 collections.

PANAMÁ. 132 (22.2–286) from 45 collections. BMNH 1860.6.18.11 (1, 162) and 1860.6.16.222 (1, 96.7); Pacific coast of Panamá; syntypes of *B. pacifici.* MCZ 12755–57 (6, 80.3–182); Pacific coast of Panamá; Hasler Expedition. MCZ 12807 (1, 194); Panamá. MCZ 29712 (1, 180); Panamá Bay; R/V ALBATROSS. MCZ 41805 (2, 190–206); Bella-Vista Beach. USNM 10116 (1, 255); Panamá. USNM 41229 (1, 232); Panamá; R/V ALBATROSS. USNM 50349 (1, 195); Panamá. USNM 65435 (1, 234); Panamá Bay; R/V ALBATROSS. USNM 76575 (1, 182); Panamá City. USNM 80993 (1, 240); Panamá City market. USNM 80994 (1, 208); Panamá City market. USNM 80995 (1, 276); Panamá City market. USNM 80996 (1, 213); Panamá City market. USNM 80997 (1, 286); Panamá City market. USNM 80998 (1, 204); Balboa. USNM 80999 (2, 186–192); Balboa. USNM 81000 (2, 244–247); Balboa. USNM 81001 (1, 280); Panamá City market. USNM 81686 (1, 22.2); Panamá City tide pools. USNM 81687 (2, 37.6–42.0); Panamá City tide pools. USNM 81688 (2, 42.7–73.8); Panamá City tide pools. USNM 82231 (2, 139–182); Chame Point. USNM 106714 (1, 163); Canal Zone, Venado Beach. USNM 111862 (3, 162–241); Canal Zone, Miraflores Locks. USNM 111864 (1, 214); Farfan Beach. USNM 111865 (1, 244); San Francisco Beach. USNM 144877 (2, 26.2–72.8); Miraflores Locks. USNM 144881 (4, 42.4–87.3); San Francisco Reef. USNM 144882-3 (4, 41.7–160); San Francisco Reef. USNM 144886–7 (18, 36.4–147); Venado and Farfan beaches. FMNH 26090–95 (6, 221–244); Panamá City market. FMNH 26096–26100 (5, 136–235); Canal Zone. FMNH 32036–39 (4, 28.0–67.4); Canal Zone. SIO 58-405 (3, 187–241); Miraflores Locks. SIO 58-450 (1, 125); Vigne Point. SIO 67-41 (1, 230); Pearl Is., Isla Pedro Gonzales. SIO 67-42 (1, 40.0); Paitilla Point. SIO 70-366 (3, 22.2–171); Venado Beach; 8°54'N, 79°36'W. UMML 26705 (2, 119–187); 8°59.5'N, 79°30.5'W; R/V PILLSBURY 482. UMML 27127 (34, 35.8–180); Venado Beach, Kobbe Army Base. USNM uncat. (1, 146); Bay of Garochine, San Miguel. GCRL V72:8403 (1, 25.0); Canal Zone, Miraflores Locks. LACM 32732-1 (1, 60.3); Panamá City; L. G. Abele 69-29. CAS SU 6872 (14, 23.6–215); Panamá.

COLOMBIA. 10 (63.6–249) from 6 collections. CAS IU 15050 (2, 148–160); Colombia. FMNH 55183 (2, 176–249); Colombia; CM 3886a-b. FMNH 55182 (1, 147); Buenaventura. USNM 217416 (1, 143); Tumaco Bay; 2°2'N, 78°46'W; 20 fms. USNM 217414 (1, 116); Buenaventura Bay, 3°32'N, 77°22'W; 5 fms. USNM 219385 (3, 63.6–204); 3°50'25"N, 77°10'30"W; 0–2 ft.

ECUADOR. 7 (138–269) from 3 collections. USNM 53486 (4, 138–192); Guayaquil. CAS IU 15049 (1, 250); Guayaquil; Landon Expedition. LACM 23609 (2, 260–269); Guayaquil; AHF 284.

PERU. 1 (36.3) from 1 collection. GCRL V74:12555 (1, 36.3); Tumbes, El Rubeo, Inter-American Hwy. km 1276; 0–1 m.

Batrachoides gilberti Meek and Hildebrand
Figure 7

Batrachoides gilberti Meek and Hildebrand, 1928: 914–915 (original description; Atlantic coast of Panamá Canal Zone; 6 specimens, 45–225 mm SL, USNM 81002, 81003), pl. 90. Fowler, 1944: 473 (Mindi Cut, Panamá; listed). Miller, 1966: 800 (Nicaragua to Panamá, entering freshwater in Deadman's Creek, Bluefields, Nicaragua). Gilbert and Kelso, 1971: 46 (Tortuguero, Costa Rica; 5 specimens, 31–146 mm SL, UF 12013). Greenfield and Greenfield, 1973: 564 (2 specimens from Belize City, 1 from freshwater in Southern Lagoon; FMNH 71317, 86557, 86558). Miller, 1976: 156 (Greenfield and Greenfield freshwater record). Collette, 1978: Batra 1 and 2 (comparisons with *B. manglae* and *B. surinamensis*; fig. of dorsal surface of head).

Diagnosis.—A moderate-sized species of *Batrachoides* (maximum size 230 mm SL); with large eyes (4.0–6.9% SL, $\bar{x}$ 5.35), 0.89–2.54 times in interorbital distance ($\bar{x}$ 1.65); reduced head squamation (extending almost to supratemporal canal, Fig. 2F); a moderate number of lateral line pores (upper (20–27) + (14–19) = 36–45, lower (19–27) + (9–15) = 33–41); a moderate number of fin rays (dorsal rays 24–26, usually 25; anal rays 22–23); a moderate number of vertebrae (usually 19 + 25 or 26 = 34 or 35); and few pectoral fin glands (0–8).

Body proportions are presented in Table 7, counts in Tables 2–5. Teeth on dentary 19–37, premaxilla 27–42, palatine 13–18 (22), and vomer 9–12.

Most similar to the eastern Pacific *B. pacifici* in body size, eye size, head squamation and most meristic characters but differs sharply in having fewer pectoral fin glands (0–8 vs. 10–16, Table 5). Also, has more teeth on the dentary, premaxilla, palatine, and vomer. Differs from the other western Atlantic species with which it may co-occur (*B. surinamensis*) in having fewer dorsal and anal fin rays (Table 2), pores in both lateral lines (Table 4), and a much larger eye.

Types.—Holotype USNM 81002 (ripe female, 225); Canal Zone, creek opposite Mindi Cut; S. E. Meek and S. F. Hildebrand; 17 Jan. 1911; D III, 26; A 23, P_1 20–21; vertebrae 9 + 26 = 35; upper lateral line 22 + 14 = 36; lower lateral line 22 + 12 = 34; P_1 glands 5–5; head squamation extending half way from first dorsal fin origin to supratemporal canal; one long supraorbital tentacle plus 6 smaller ones over each eye, several of larger tentacles branched at base; scattered filaments on interorbital region anterior to middle of eye; head length 90.9 mm; head width 70.6 mm; orbit diameter 9.5 mm; interorbital distance 22.0 mm; snout–2D 110 mm; snout–A 125 mm; P_1 48.5 mm: P_2 33.6 mm. Paratypes: USNM 81003 (5, 115–192); Canal Zone, small stream flowing into French Canal near Mindi Cut; S. E. Meek and S. F. Hildebrand; 17 Jan. 1911.

Size and Fecundity.—A medium-sized species, reaching 230 mm SL (FMNH 86513, Belize City). Males appear to be ripening by 161 mm SL, females by 188 mm. A 192-mm female from Panamá had 398 eggs, 4.4–5.3 mm in diameter ($\bar{x}$ 4.86).

Food Habits.—Five specimens (161–213 mm SL) were examined, all contained food in the intestines. Xanthid and portunid crabs were present in 3 out of 5. Shrimps (*Macrobrachium*) were present in 3 specimens from a creek opposite Mindi Cut in the Panamá Canal Zone. Three gastropods (of 2 species) were present in a specimen from Belize. Fish bones were present in 2 specimens.

Range.—Found from the Caribbean side of the Yucatán Peninsula (Chetumal, Quintana Roo and Belize City) south along the coast of Central America to the

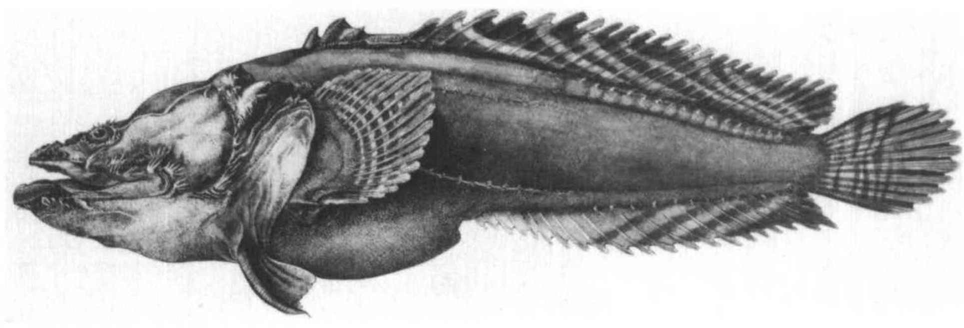

Figure 7. *Batrachoides gilberti*, holotype, USNM 81002, 225 mm SL, Panamá Canal Zone, from Meek and Hildebrand (1928: pl. 90).

Canal Zone in Panamá (Fig. 3). Previously known only as far north as Tortuguero, Costa Rica (Gilbert and Kelso, 1971) and Belize City (Greenfield and Greenfield, 1973). Enters freshwater at Southern Lagoon, Belize (Greenfield and Greenfield, 1973), Temash River (32 km upstream, FMNH 86557), and Deadman's Creek, Bluefields, Nicaragua (Miller, 1966).

Material Examined.—41 specimens (23.2–230 mm SL) from 18 collections.

MÉXICO. 2 (63.4–108) from 1 collection. GCRL 4621 (2, 63.4–108); Quintana Roo, Chetumal, S side of harbor; 0–0.6 m.

BELIZE. 6 (38.7–230) from 6 collections. FMNH 71317 (1, 188); Belize City. FMNH 86558 (1, 150); off Belize City. FMNH 86556 (1, 103); off Belize City. FMNH 86555 (1, 38.7); southern Lagoon, Gales Point. FMNH 86557 (1, 126); Toledo District, Temash R; .25 mi from Crique Sarco. FMNH 86513 (1, 230); Belize City harbor.

GUATEMALA. 4 (57.8–223) from 3 collections. GCRL V70: 4405 (2, 57.8–65.3); Izabel, Bahia de Matias de Galvez; 15°44'56"N, 88°37'40"W; 0–0.9 m. UMMZ 197284 (1, 125); Izabel, Río Frio, just above mouth in El Golfete; 15°41'20"N, 88°54'30"W. AMNH 35033 (1, 223); Izabel, Río Dulce just below Marimonte.

HONDURAS. 17 (23.2–138) from 3 collections. FMNH 84545 (1, 60.9); Brus Lagoon. FMNH 84546 (2, 23.2–40.6); Brus Lagoon. FMNH 84549 (14, 31.9–138); Brus Lagoon.

NICARAGUA. 2 (203–213) from 2 collections. ANSP 123884 (1, 203); Prinzepolka. UMML UMIM 3877 (1, 213); Bluefields, Deadman's Creek.

COSTA RICA. 4 (30.5–146) from 1 collection. UF 12013 (4, 30.5–146); Limon Province, Tortuguero Lagoon.

PANAMÁ. 6 (115–225) from 2 collections. USNM 81002 (1, 225); Canal Zone, creek opposite Mindi Cut, holotype. USNM 81003 (5, 115–192); Canal Zone, small stream flowing into French Canal, near Mindi Cut; paratypes.

Batrachoides manglae Cervigón
Figure 8

Batrachoides manglae Cervigón, 1964: 1–4 (original description; Margarita and Cubagua islands, Venezuela), fig. Cervigón, 1965: 69 (Venezuela; listed). Cervigón, 1966: 858–860 (description; Venezuela; fig. 367). Mago Leccia, 1970: 86 (Venezuela; listed). Cedeño Campos, 1972 (osteology). Collette, 1978: Batra 1 (description, range, figs).

Diagnosis.—A small species of *Batrachoides* (maximum size 215 mm SL); with large eyes (5.1–8.2% SL, $\bar{x}$ 6.76), 0.60–1.84 times in interorbital distance ($\bar{x}$ 1.03); reduced head squamation (extending up to supratemporal canal, Fig. 2G); few lateral line pores (upper (16–26) + (9–15) = 29–40, lower (19–27) + (3–11) = 24–37); few fin rays (dorsal rays 21–24, usually 22–23; anal rays 19–21, usually 20); few vertebrae (usually 9 + 22 or 23 = 31 or 32); and a moderate number of pectoral fin glands (4–11, usually 6–11).

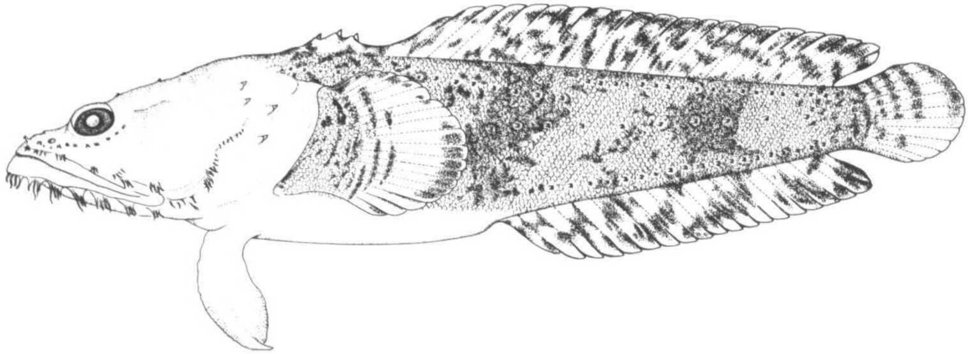

Figure 8. *Batrachoides manglae*, ANSP 102200, 176 mm SL, Venezuela, Araya Peninsula, drawn by Keiko Hiratsuka Moore.

Body proportions are presented in Table 8, counts in Tables 2–5. Teeth on dentary 15–22, premaxilla 21–35, palatine 11–13, and vomer 6–9, usually 6 or 7. Most similar to the freshwater *B. goldmani* in body size, head squamation and most meristic characters but differs sharply in having fewer pectoral fin glands (4–11 vs. 13–17, Table 5). Differs from the other two Atlantic species (*B. gilberti* and *B. surinamensis*) in having lower counts of fin rays, lateral line pores, and vertebrae.

Types.—Holotype Mus. Hist. Nat. La Salle 875 (1, 170); Venezuela, Nueva Esparta, Punta de Piedras; 10 Aug. 1964; D III, 22; A 20; P_1 20–22 (counts from Cervigón, 1964: 2). Paratypes MHNLS (1, 150) taken with holotype. MHNLS (1, 105); Isla de Cubagua; 18 June 1963. UPR 2434 (1, 93).

Size and Fecundity.—A small species, reaching 215 mm SL (ANSP 102200, Venezuela, Araya Peninsula). Males showed ripening testes by about 108 mm SL, the only mature female is 148 mm and appears to have begun spawning. This 148-mm female from the Araya Peninsula, Venezuela had 114 eggs, 2.2–3.0 mm in diameter ($\bar{x}$ 2.60).

Food Habits.—Five specimens (108–164 mm SL) were examined, all contained crabs. Six families of crabs were found: Paguridae in 4 of 5 (*Pagurus* and *Paguristes* in gastropod shells), Majidae (*Mithrax*, probably *M. pleuracanthus*), Porcellanidae, Portunidae (possibly *Callinectes marginatus*), Xanthidae (*Panopeus*), and Parthenopidae (*Heterocrypta granulata*). A penaeid shrimp (*Penaeus schmitti*), was found in one specimen, but is in such good condition that it may have been eaten in the seine. Gastropods were found in 3 of 5 specimens but most, if not all, were homes for hermit crabs. Cervigón (1966) reported gastropods and decapods (*Callinectes*) in the intestinal tract.

Range.—Restricted to a small part of central Venezuela, the Araya Peninsula on the mainland and the islands of Margarita and Cubagua offshore (Fig. 3). Inhabits mangrove swamps of high salinity (up to 39‰) according to Cedeño Campos (1972).

Material Examined.—28 specimens (18.0–215 mm SL) from 11 collections from the Araya Peninsula, Isla Margarita, and Isla Cubagua, Venezuela. ANSP 102200 (5, 148–215); Sucre, Araya Peninsula between Punta Horno and Punta Cardon; W. A. Lund 213. UDONECI uncat. (1, 114); Sucre, Güira de la Playa Carupano. UPR 2019 (1, 132); Isla Margarita, Punta de Piedras. UDONECI 162 (1, 118); Isla Margarita. GCRL V77:15516 (4, 20.2–99.2); Isla Margarita, Boca del Río. GCRL V77:15518 (3, 64.7–82.0) and GCRL V77:15517 (2, 45.9–54.8); Isla Margarita, Laguna de la Restinga. GCRL

V78:15862 (6, 75.6–97.0); Isla Margarita, 10 km W of Boca del Río. USNM 218893 (1, 108) and USNM 218894 (1, 18.0); Isla Margarita, Bahia Mangles, Boca del Río. GCRL V77:15520 (3, 68.4–96.4); Isla Cubagua between Pt. Charagatos and Pt. Brasil.

Batrachoides goldmani Evermann and Goldsborough
Figure 9

Batrachoides goldmani Evermann and Goldsborough, 1902: 159 (original description; Río Usumacinta, México, 260 mm SL, USNM 50006), fig. 8. Meek and Hildebrand, 1928: 913–914 (description based on re-examination of holotype). Jordan, Evermann, and Clark, 1930: 487 (listed). Miller, 1966: 778, 800 (restricted to Río Usumacinta basin in México and Guatemala).

Diagnosis.—A small species of *Batrachoides* (maximum size 216 mm SL); with large eyes (5.1–8.2% SL, $\bar{x}$ 6.67), 0.64–2.03 times in interorbital distance ($\bar{x}$ 1.00); moderate head squamation (extending just anterior to supratemporal canal, Fig. 2H); few lateral line pores (upper (18–25) + (10–17) = 30–40, lower (17–21) + (9–13) = 28–32); few fin rays (dorsal rays 21–23, usually 22–23; anal rays 19–21, usually 20); few vertebrae (usually 9 or 10 + 22 = 31 or 32); and many pectoral fin glands (13–17).

Body proportions are presented in Table 8, counts in Tables 2–5. Teeth smaller, longer, thinner, and more pointed than in any other species in the genus, dentary 30–41, premaxilla 37–64, palatine 16–20, and vomer 8–15, increasing to 30–32 in large adults (193–216 mm SL) by adding a second row of teeth.

Most similar to the western Atlantic *B. manglae* in body size, head squamation, and low meristic values but differs sharply in having more pectoral fin glands (13–17 vs. 4–11, Table 5).

Types.—Holotype USNM 50006 (1, 216); México, Tabasco, Río Usumacinta at Montecristo (about 17°45′N, 91°45′W); E. W. Nelson and E. A. Goldman; 7 May 1900; D III, 24; A 21; P_1 18–18; vertebrae 9 + 24 = 33; P_1 glands 5–5; head squamation extending anterior almost to supratemporal canal; no supraorbital tentacles but orbital region badly dried; some scattered interorbital filaments detectable; head length 84.3 mm; head width 61.5 mm; orbit diameter 10.9 mm; interorbital distance 22.1 mm; snout–2D 106 mm; snout–A 124 mm; P_1 55.4 mm; P_2 31.3 mm.

Size and Fecundity.—A small species, reaching 216 mm SL (USNM 50006, México, Río Usumacinta). The only apparently ripe male is the large 216-mm holotype, females appear to be ripening by 106 mm. A 193-mm female from Río de la Pasión had 88 eggs, 3.8–4.6 mm in diameter ($\bar{x}$ 4.06).

Food Habits.—Six specimens (71.8–216 mm SL) were examined; all contained food in the intestine. Crab fragments were present only in the holotype from Tabasco, México. Four of the 5 specimens from the Río de la Pasión in Guatemala contained fish bones or scales. The premaxilla in one set of gut contents had a very long premaxillary projection and appears referable to the gerreid *Eugerres mexicanus*. The smallest *B. goldmani* contained a 21.5 mm eleotrid of the genus *Microeleotris* (considered a synonym of *Leptophilypnus* by Miller, 1966). Two of the 5 specimens from the Río de la Pasión contained insect fragments.

Range.—A freshwater species thought to be restricted to the basin of the Río Usumacinta (Miller, 1966) in the states of Chiapas and Tabasco, México and El Petén and Alta Verapaz, Guatemala (Fig. 3). Recently discovered by ecologists from the University of Michigan in a tributary (Río Mescalpa) to the next river to the west of the Usumacinta, Río Grijalva. The Usumacinta-Grijalva is a major division of the Usumacinta Province as delimited by Miller (1966: 777), so the

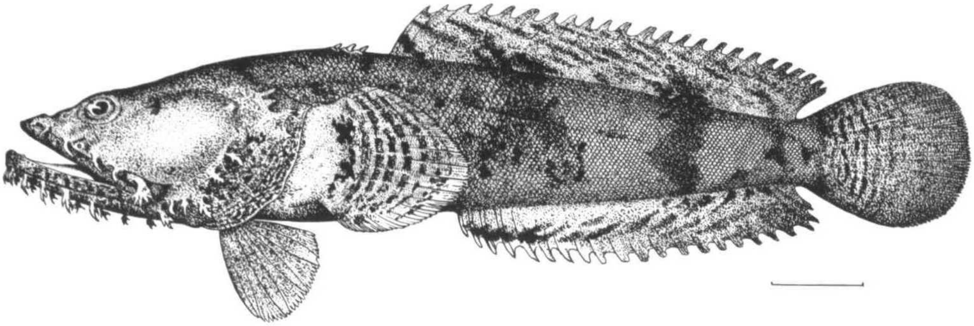

Figure 9. *Batrachoides goldmani*, holotype, USNM 50006, 216 mm SL, México, Río Usumacinta, drawn by A. H. Baldwin.

occurrence of *B. goldmani* in the Grijalva is hardly surprising. Many of the localities for *B. goldmani* can be found on the map compiled by Carl L. Hubbs and Henry van der Schalie (Collette, 1974b: 613).

Material Examined.—29 specimens (37.8–216 mm) from 18 collections in the Río Usumacinta Province of México and Guatemala.

MÉXICO. 2 (67.5–216 mm) from 2 collections. USNM 50006 (1, 216); Tabasco, Río Usumacinta, Montecristo; holotype. UMMZ 203318 (1, 67.5); Tabasco, Río Mescalpa at Huimanguillo, 21 km S of Cárdenas.

GUATEMALA. 27 (37.8–197 mm) from 16 collections. ANSP 127716 (1, 90.7); Sayaxché; Usumacinta Expedition. UMML UMIM 4035 (1, 100); Río de la Pasión at Sayaxché. UMMZ 144152 (1, 44.5); Petén, Arroyo Subin, Santa Teresa, 13 mi S of La Libertad, trib. of Río de la Pasión and Río Usumacinta. UMMZ 144153 (1, 197); Petén, Río Sta. Amelia above mouth into Río de la Pasión between Sta. Amelia and Tres Islas. USNM 219384 (1, 193); Petén-Alta Verapaz line; Río de la Pasión from San Diego to 1 mi above, between El Cambio and Cancuen. UMMZ 144155 (1, 127); Alta Verapaz; Río de la Pasión between Rodal de Embudo and Rodal Grande, between Río Senimlatoc and Río San Simón. UMMZ 144156 (6, 70.3–151); mouth of first arroyo tributary to upper Río de la Pasión (=Río Chajmayíc). UMMZ 144157 (2, 37.8–51.8); Petén; Arroyo San Martin, close to mouth into Río de la Pasión, east of Sayaxché. USNM 219383 (4, 71.8–115); in and just above mouth of first arroyo tributary to Río de la Pasión (=Río Chajmayíc) from east below Arroyo San Simón. UMMZ 144159 (2, 51.7–175); Petén, Río de la Pasión, immediately above mouth of Arroyo de Petexbatúm at Sayaxché. UMMZ 188039 (1, 44.2); Petén, Arroyo Tamarindo 0.5 km above mouth in Laguna Petexbatúm; 16°24′15″N, 90°11′20″W. UMMZ 190093 (1, 53.7); Petén, Arroyo Negro from mouth in Río de la Pasión up 300 m; 16°33′20″N, 90°18′40″W. AMNH 25623 (1, 121); Petén, Arroyo El Porvenir, 3 km above mouth in Río de la Pasión. AMNH 25279 (1, 79.7); Alta Verapaz; Arroyo Chiquibul downstream from campsite, Río Icvolay. AMNH 24532 (1, 75.9); Alta Verapaz, arroyo flowing W into Río de la Pasión, 8 km downstream of Sebol. AMNH 32028 (2, 57.3–67.7); Petén, Arroyo Bejucal 125 m above mouth on right bank Río de la Pasión.

Batrachoides liberiensis (Steindachner)

Batrachus liberiensis Steindachner, 1867: 521–523 (original description, Monrovia, Liberia), pl. 1, fig. 3. Monod, 1927: 737 (Cameroons; *B. beninensis* a synonym of *B. liberiensis*). Roux, 1957: 220–221 (Congo; description), 355 (fig. 93). Poll, 1959: 332–333 (Congo and Angola; description, 19 specimens 55–197 mm; fig. 112).

Batrachoides pacifici. not of Günther. Günther, 1869: 435 (*B. liberiensis* considered conspecific with *B. pacifici*). Ehrenbaum, 1915: 80 (Cameroons, 2 specimens).

Batrachoides beninensis Regan, 1915: 130 (original description; Lagos, Nigeria; 3 specimens, 145–180 mm SL, BMNH 1914.11.2.67–9). Monod, 1927: 737 (*B. beninensis* a synonym of *B. liberiensis* based on re-examination of types by J. R. Norman). Fowler, 1936: 1077 (description after Regan).

Batrachoides liberiensis. Fowler, 1936: 1331–1332 (description). Irvine, 1947: 219 (Accra, Ghana; description, fig. 133). Cadenat, 1950: 277–278 (Senegal; description; fig. 221–222). Blache, Cadenat, and Stauch, 1970: 401 (in key; figs. 1029a, b). Roux 1971a: 639–641 (Guinée to Angola; description; 12 specimens from MNHN, NHMV, RMNH, USNM), figs. 2, 3, 4, and 9. Roux,

Table 8. Morphometric comparison (as % SL) of *Batrachoides manglae*, *B. goldmani*, and *B. liberiensis*

Character	*B. manglae*					*B. goldmani*					*B. liberiensis*				
	Min.	Max.	$\bar{x}$	SE	N	Min.	Max.	$\bar{x}$	SE	N	Min.	Max.	$\bar{x}$	SE	N
Standard Length (mm)	68.4	215	113.1	9.1	20	70.3	216	121.6	10.2	19	80.7	200	126.2	7.1	23
Head Length	37.1	43.5	39.39	0.33	20	38.4	43.0	40.24	0.26	19	33.3	39.9	37.17	0.32	23
Head Width	26.8	34.2	30.12	0.46	20	28.4	32.9	30.47	0.28	19	24.3	36.5	29.38	0.56	21
Orbit Diameter	5.0	8.2	6.76	0.18	20	5.1	8.2	6.67	0.24	19	3.1	4.8	3.78	0.10	23
Interorbital Distance	4.5	10.8	6.70	0.38	20	5.0	10.2	7.00	0.30	19	7.8	12.2	9.73	0.24	23
Snout–2D	38.2	51.4	47.29	0.64	20	46.2	49.8	48.30	0.23	19	44.0	49.2	45.94	0.33	23
Snout–A	52.0	60.2	55.82	0.46	20	54.0	58.9	56.49	0.29	19	52.0	59.0	53.81	0.35	23
Pectoral Length	19.6	24.0	21.96	0.28	20	20.2	25.7	22.93	0.37	19	19.2	26.2	21.52	0.31	23
Pelvic Length	14.8	18.8	16.96	0.26	20	14.5	18.8	17.08	0.27	19	12.6	18.4	15.86	0.32	23

1971b: 850, 852 (Liberia, Ghana, Nigeria; description; 4 specimens, 90–200 mm SL; USNM 205067–70).

Diagnosis.—The smallest species of *Batrachoides* (maximum size 200 mm SL); with small eyes (3.1–4.8% SL, $\bar{x}$ 3.78), 1.79–3.42 times in interorbital distance ($\bar{x}$ 2.62); reduced head squamation (extending about half way from dorsal origin to supratemporal canal, Fig. 2I); a moderate number of lateral line pores (upper (16–25) + (12–19) = 30–40, lower (15–26) + (11–17) = 34–42); a moderate number of fin rays (dorsal rays 25–26, usually 25; anal rays 21–23, usually 22–23); a moderate number of vertebrae (usually 9 + 25 or 26 = 34 or 35); and many pectoral fin glands (13–15).

Body proportions are presented in Table 8, counts in Tables 2–5. Teeth on dentary 20–25, premaxilla 28–40, palatine 11–16, and vomer 7–10 (18).

Batrachoides liberiensis is a small species resembling the western Atlantic *B. manglae* and freshwater *B. goldmani* and agrees with them in having few upper lateral line pores. However, *B. liberiensis* resembles the western Atlantic *B. gilberti* and the eastern Pacific *B. pacifici* in having moderate numbers of lower lateral line pores, fin rays, and vertebrae. It resembles *B. goldmani* and *B. pacifici* in moderately high numbers of pectoral fin glands (13–15, compared to 13–17 and 10–16 for the other two species). *B. liberiensis* and *B. goldmani* have the most extensive coverage of fine filaments on the top of their heads (Figs. 2H, 2I).

Types.—*Batrachus liberiensis* Steindachner, holotype NHMV 5558 (1, 97.8); Liberia, Monrovia; D III, 25; A 22; P_1 20–20; vertebrae 9 + 25 = 34; upper lateral line 20 + 15 = 35; lower lateral line 22 + 15 = 37; P_1 glands 14–14; head squamation extending forward about halfway from first dorsal fin origin to supratemporal canal; 5 short, stubby tentacles over each eye; dorsal surface of head covered with fine filaments; head length 37.4 mm; head width 28.7 mm; orbit diameter 3.7 mm; interorbital distance 9.0 mm; snout–2D 42.7 mm; snout–A 53.5 mm; P_1 19.7 mm; P_2 16.1 mm.

Batrachoides beninensis Regan. Lectotype, herein selected, BMNH 1914.11.2.67 (1, 168); Nigeria, Lagos; J. Cadman; D III, 25; A 22; P_1 20–20; vertebrae 9 + 26 = 35; upper lateral line 26 + 13 = 39; lower lateral line 24 + 16 = 40; P_1 glands 15–14; head squamation extending forward about halfway from first dorsal fin origin to supratemporal canal; 3 short, stubby tentacles over each eye; dorsal surface of head covered with fine filaments; head length 59.8 mm; head width 48.3 mm; orbit diameter 6.6 mm; interorbital distance 16.7 mm; snout–2D 75.3 mm; snout–A 90.0 mm; P_1 38.8 mm; P_2 29.4 mm. Paralectotypes BMNH 1914.11.2.68–69 (2, 145–180); Nigeria, Lagos; J. Cadman.

Size and Fecundity.—This is probably the smallest species in the genus, reaching 200 mm SL (USNM 219841; Ghana). Males appear to be ripening by 170 mm SL, a 122-mm female from Ghana appears to be ripe. The 122-mm female had 93 eggs, 3.3–4.5 mm in diameter ($\bar{x}$ 3.88).

Food Habits.—Five specimens (103–170 mm SL) were examined, all contained crabs. The family Goneplacidae was present in 3 of 5, identifiable to the genus *Pilumnoplax* in one case. Three other families of crabs were found: Portunidae (?), Xanthidae, and Dorippidae (genus *Ethusa*). Fish bones were present in one stomach.

Range.—*Batrachoides liberiensis* is the only non-American species of the genus and the only representative of an American genus of toadfishes found in the eastern Atlantic ocean. It is found along the coast of the Gulf of Guinea from

Table 9. Two factor analysis of variance summary table for *Batrachoides* egg size

Source of Variation	Sums of Squares	D.F.	Mean Square
Total	186.2666	179	
Cells	172.3005	17	
Factor A (individual)	170.497	8	21.3121
Factor B (left vs. right)	0.0534	1	0.0534
A × B (interaction)	1.7501	8	0.2188
Within cells (error)	13.9650	162	0.0862

Senegal (Cadenat, 1950) and Guinea (Roux, 1971a) south to Mangue Grande in northern Angola (6°40′S, 120°36′E; Poll, 1959).

Material Examined.—38 specimens (43.9–200 mm SL) from 20 collections from the Gulf of Guinea.

SIERRA LEONE. 1 (145) from 1 collection. USNM 205067 (1, 145); 7°22′N, 12°38′W; 20 m, Guinean Trawling Survey I-11-1; R/V RAFALE.

LIBERIA. 7 (80.7–172) from 6 collections. USNM 193648 (2, 80.7–127); Liberia. USNM 193663 (1, 121) and USNM 193619 (1, 117); off St. Paul River; 4–7 fms. USNM 193845 (1, 172); Bushrod I. USNM 205068 (1, 92.2); 6°18′N, 10°49′W; 20 m; Guinean Trawling Survey I-14-1; R/V RAFALE. NHMV 5558 (1, 97.8); holotype of *Batrachus liberiensis* Steindachner; Monrovia; 1867.

GHANA. 19 specimens (90.5–200) from 10 collections. USNM 205069 (1, 115); 4°52′N, 1°39′W; 28 m; Guinean Trawling Survey I-29-2; R/V THIERRY. USNM 219392 (1, 111); Shama Bay; G. W. Bane 805. USNM 219841 (1, 200); Dix Cove near Axin; G. W. Bane 808. USNM 219394 (3, 96.0–114); Shama Bay; G. W. Bane 821. USNM 219842 (2, 114–122); Shama Bay; G. W. Bane 825. USNM 207957 (3, 124–131); Shama Bay; G. W. Bane 826. UMMZ 202525 (1, 108); Shama Bay; G. W. Bane 827. ANSP 140358 (1, 116); Shama Bay; G. W. Bane 835. USNM 219393 (5, 90.5–170); Western Ghana; G. W. Bane 837. FMNH 83861 (1, 105); Appam; G. W. Bane 879.

NIGERIA. 11 (43.9–195) from 3 collections. USNM 205070 (1, 195); 6°15′N, 4°17′E; 20 m; Guinean Trawling Survey II-38-1; R/V THIERRY. UMML 16986 (7, 43.9–96.4); 5°05′N, 4°59′W; 12 fms; R/V PILLSBURY 48. BMNH 1914.11.2.67 (1, 168) lectotype and BMNH 1914.11.2.68–69 (2, 145–180); paralectotypes of *Batrachoides beninensis* Regan; Lagos; 10–35 fms.

DISCUSSION

Five topics are included in this section—fecundity, food habits, parasites, zoogeography, and relationships.

Fecundity

In order to determine if there is a difference in egg diameter between individuals or right and left ovary positions a sample of 10 eggs was measured from each ovary of 9 females representing all 9 species of *Batrachoides*. A two factor analysis of variance was performed using individual (species, 9 levels) as the first factor, and ovary position (2 levels, right or left) as the second factor. The results of the testing procedure are presented in Table 9.

There is a highly significant difference between individuals (first factor) with regard to mean egg diameter. The calculated value of the F statistic is 247. Average egg diameters are presented in Table 10. The 201 mm specimen of *B. waltersi* had the largest mean egg diameter (6.10 mm) and the 148 mm specimen of *B. manglae* had the smallest (2.60 mm). Our test results show no significant difference ($\alpha = .05$) between ovary position (second factor) with regard to mean egg diameter. The calculated value of the F statistic was 0.619 ($P < 0.25$). There is a slightly significant interaction between the two factors ($F = 2.54$, $.025 > P > .01$). From the two factor analysis of variance, we conclude: 1) the mean egg

Table 10. Mean egg diameters and numbers of eggs of species of *Batrachoides*

		Left		Right		Left plus Right	
Species	SL (mm)	$\bar{x}$ Egg Size (n = 10)	No. of Eggs	$\bar{x}$ Egg Size (n = 10)	No. of Eggs	$\bar{x}$ Egg Size (n = 20)	Total No. of Eggs
B. boulengeri	352	5.52	332	5.41	256	5.45	588
B. surinamensis	225	4.09	229	3.96	222	4.02	451
B. pacifici	204	4.56	96	4.29	106	4.42	202
B. waltersi	201	6.26	88	5.95	94	6.10	182
B. gilberti	192	4.81	177	4.92	221	4.86	398
B. manglae	148	2.62	63	2.57	51	2.60	144
B. liberiensis	122	3.81	44	3.94	49	3.88	93
B. goldmani	106	4.08	54	4.04	34	4.06	88
B. walkeri	170	4.16	87	3.87	85	3.69	172

diameter is significantly different ıor individual females of different species (and different sizes), 2) there is no difference in mean egg diameter of right and left ovaries, 3) there is a slightly significant interaction between the two factors.

As stated in conclusion one above, our sample of individual females represented different species and sizes of *Batrachoides*. In order to determine which aspects of egg production and development are correlated with the size of the individual females, correlation analysis was performed on the variables, size of female, mean egg diameter, and total number of eggs. Simple linear correlation coefficients were calculated from three correlations; total number of eggs per female vs. mean egg diameter, standard length of female vs. mean egg diameter, and standard length of female vs. total number of eggs. Results are presented in Table 11. In order to test the null hypotheses that the population correlation coefficients ρ (rho) = 0, calculated values of r were compared to critical values of r (α = .05) for their respective degrees of freedom (n − 2 = 7 in each case). The hypothesis that $\rho = 0$ (no significant correlation) was accepted for the first two correlations, total number of eggs per female vs. mean egg diameter and standard length of female vs. mean egg diameter. However, the hypothesis that $\rho = 0$ for standard length of female vs. total number of eggs was rejected. There is a significant correlation between size of female and total number of eggs.

From the results of correlation tests we conclude that size of eggs is not correlated with size of female or with total number of eggs per female. We also conclude that the total number of eggs present is correlated with the size of the female. From the results of the two factor analysis of variance and the correlation procedure, we conclude: 1) both right and left ovaries mature at the same time; and 2) larger individuals produce more eggs rather than larger eggs. This implies that mature *Batrachoides* eggs tend to be the same size and that species of *Batrachoides* mature at different sizes.

Table 11. Results of simple linear correlation concerning average egg size, total number of eggs, and standard length of female *Batrachoides*

X	Y	n	r	D.F.	Significance of Correlation (α = .05)
Total number of eggs	Mean egg diameter	9	.45	7	NS
SL of female	Mean egg diameter	9	.56	7	NS
SL of female	Total number of eggs	9	.89	7	*

Scanty data on three species of toadfishes show their eggs to be comparable in size with those of *Batrachoides*. Gudger (1910) reported a range of 4–6 mm (average 5 mm) for *Opsanus tau*, Breder (1941) found a range of 3.9–4.4 ($\bar{x}$ 4.1) for 12 eggs of *O. beta*, and Arora (1948) noted that eggs of *Porichthys notatus* averaged 6 mm in diameter. Gudger counted the number of eggs found in eight nests of *O. tau*: 22, 181, 301, 340, 361, 373, 624, and 723. Based on the large egg size and small size of the ovary, he estimated that a female *O. tau* would lay about 100 eggs and that higher numbers were due to several females laying eggs in the same nest.

Food Habits

The guts of 5–10 specimens of each species were examined (the only specimen of *B. walkeri* had an empty gut). Little food was found in stomachs of *Batrachoides* and in at least one case where food was present in the stomach (a large penaeid shrimp), it appeared that the fish may have eaten the shrimp while they were in the seine together. Most gut contents were in the intestine, particularly in the short, very wide large intestine. A number of individuals seemed to have a blockage, just anterior to the anus, caused by the build-up of crab carapaces and chelae, gastropod shells, and fish bones. Detailed information is presented in each species account, a summary in Table 12. Crabs are the primary item of food in all species except the freshwater *B. goldmani*. In the other seven species, crabs were present in 60–100% of the individuals with food in the gut. Twelve families of crabs were identified, xanthids being found in all seven marine *Batrachoides*. Shrimps were important in the three western Atlantic species. Gastropod shells were found in four species but many of these appear to have been eaten because they contained hermit crabs. A stomatopod was found in one *B. surinamensis*. Insects and fishes comprised the major items in the freshwater *B. goldmani*. Fishes were also found in most of the marine species.

These brief notes on the food of *Batrachoides* may be compared to three other studies on toadfish food, those by Schwartz and Dutcher (1963), and McDermott (1965) on *Opsanus tau* in Chesapeake Bay and New Jersey waters, respectively and that by Cárdenas (1977) on *Halobatrachus didactylus* in Cadiz Bay, Spain. Food items were present in the intestines of these two species and largely absent from the stomachs as in *Batrachoides*. Crustaceans, particularly crabs, were the dominant group of food organisms by both frequency and weight for both *O. tau* and *H. didactylus*. In Chesapeake Bay, xanthid crabs (*Rhithropanopeus harrisii* and *Eurypanopeus depressus*) were the major food of *O. tau* (46.0 and 16.6% frequency; 27.1 and 12.9% volume, respectively). In New Jersey waters, xanthid crabs (*Neopanope texana* and *Eurypanopeus depressus*) and hermit crabs (*Pagurus* spp.) were dominant (66.4, 25.3, and 49.5% frequency, respectively). Crustaceans formed 55.9% of the diet of *H. didactylus* by frequency, 60.7% by volume. Cárdenas found 14 families of crabs in the 898 digestive tracts of *H. didactylus* from Cadiz compared to the 12 families we found in 44 digestive tracts from eight species of *Batrachoides*. Portunids (*Macropipus* spp.) and hermit crabs were the major groups of crabs found in *H. didactylus*, xanthids in *Batrachoides*. Fishes and mollusks were minor components of the diet in *O. tau*, *H. didactylus*, and all the species of *Batrachoides* (except the freshwater *B. goldmani*).

Parasites

Parasitic nematodes were found in the intestines of specimens of four species of *Batrachoides*: *B. boulengeri* from Panamá Bay, *B. pacifici* from Panamá and

Table 12. Gut contents of *Batrachoides* species (as % specimens with food)

Area	Eastern Pacific			Western Atlantic			Freshwater	E. Atlantic
Species	*B. boulengeri*	*B. waltersi*	*B. pacifici*	*B. surinamensis*	*B. gilberti*	*B. manglae*	*B. goldmani*	*B. liberiensis*
N (with food)	4	5	5	9	5	5	6	5
CRABS	75	100	100	67	60	100	17	100
Porcellanidae			60			20		
Petrolisthes			40					
Paguridae		40				80		
Paguristes						20		
Pagurus						20		
Dorippidae								20
Ethusa								20
Leucosiidae		20						
Persephona		20						
Calappidae				22				
Hepatus				22				
Portunidae	50			22	20	20		20
Callinectes					20	20		
Cronius				11				
Xanthidae	75	20	80	11	20	20		20
Panopeus	50		20			20		
Goneplacidae								60
Pilumnoplax								20
Pinnotheridae		20		11				
Pinnotheres		20						
Palicidae				11				
Palicus				11				
Majidae						40		
Mithrax						20		
Parthenopidae						20		
Heterocrypta						20		
SHRIMPS	0	0	0	67	60	20	0	0
Penaeidae				11		20		
Penaeus						20		
Palaemonidae				11	60			
Brachycarpus				11				
Macrobrachium					60			
Alpheidae				11				
STOMATOPODS	0	0	0	11	0	0	0	0
GASTROPODS	0	60	20	0	20	60	0	0
INSECTS	0	0	0	0	0	0	33	0
FISHES	50	20	0	11	40	0	67	20
Gerreidae							17	
Diapterus							17	
Eleotridae							17	
Microeleotris							17	
Diodontidae	25							
Chilomycterus	25							

Table 13. Numbers of genera and species found in various parts of the world (total 19 genera, 64 species, some genera occur in more than one region; number in parentheses indicates freshwater species)

Area	Genera	Species
W. Atlantic	7	25 (+3)
South Africa	5	8
E. Pacific	4	15
Gulf of Guinea	3	4
Indo-West Pacific	3	9

Colombia, *B. waltersi* from El Salvador, and *B. surinamensis* from Honduras, Guyana, and northern Brazil. They have been identified as *Hysterothylacium reliquens* (Norris and Overstreet), family Anisakidae by Dr. Robin M. Overstreet and Mr. Thomas L. Deardorff (pers. comm.). This nematode was described (Norris and Overstreet, 1975) from several species of fishes from the northern Gulf of Mexico including one toadfish, *Opsanus beta* (Goode and Bean). A related nematode, *H. habena* (Linton), is known from the Atlantic Coast *Opsanus tau* (Linnaeus). The revised genus *Hysterothylacium* contains about 47 species of nematodes parasitic in marine teleosts (Deardorff and Overstreet, 1981).

Zoogeography

The distribution of the three subfamilies of toadfishes and of the species of the genus *Batrachoides* deserve comment. The two most specialized subfamilies, the luminous toadfishes (Porichthyinae) and the venomous toadfishes (Thalassophryninae) are endemic to the New World. The generalized subfamily Batrachoidinae is worldwide. The major center of diversity for the entire family is the western Atlantic (Table 13) where 7 genera and 25 species are found (plus at least 3 freshwater species of Atlantic origin). With regard to species, the second most diverse area is the eastern Pacific with 15 species in 4 genera. With regard to genera, the next most diverse area is South Africa with 5 endemic genera currently recognized (Smith, 1952) for only 8 species. This pattern is different from that of many warm water marine fish groups, which have their greatest diversity in the Indo-Australian Archipelago. Part of the explanation may be ecological; most genera of toadfishes are inhabitants of sand and mud bottoms, not coral reefs (except *Sanopus*). A more complete explanation must await additional study of the five genera endemic to South Africa.

Batrachoides is the only genus of the Batrachoididae to have species in both the Old and New worlds. *B. liberiensis*, the only Old World species, is confined to the Gulf of Guinea from Senegal south to northern Angola. It may be the most generalized species in the genus (see relationships section). There are three western Atlantic species (Fig. 3), the widespread *B. surinamensis* found from Honduras south to Salvador, Brazil, *B. gilberti* from Yucatán to Panamá, and *B. manglae* which is restricted to high salinity mangrove swamps of the islands of Cubagua and Margarita and the Araya Peninsula in central Venezuela. One species has invaded freshwaters and is known from the Río Usumacinta-Grijalva rivers of the Usumacinta Province of Miller (1966). A large number of other marine derivatives are present in the Usumacinta Province including the halfbeak *Hyporhamphus mexicanus* Alvarez and the needlefish *Strongylura hubbsi* Col-

lette. Four species occur in the eastern Pacific. *B. boulengeri* from the Bay of Panamá is a geminate species of *B. surinamensis*. *B. pacifici* is a geminate species of *B. gilberti* and occurs from the Panamá Canal Zone south to northern Peru, *B. waltersi* extends from the Gulf of Nicoya, Costa Rica north to Acapulco, México. The only specimen of *B. walkeri* was collected in the Bay of Panamá with a specimen of *B. boulengeri*.

Relationships

In order to objectively resolve the problem of phyletic relationships among the species of *Batrachoides*, we subjected our data to a cladistic analysis utilizing a computer program (WAGNER 78) written by J. S. Farris (following Farris, 1970 and Farris, Kluge, and Eckardt, 1970).

Evaluating character states is an important component of cladistic analyses and has been a major difficulty for us. Other groups of toadfishes which have been studied (Porichthyinae, Thalassophryninae, *Sanopus*) represent more specialized forms. Based on its extensive squamation and full complement of opercular and subopercular spines, *Batrachoides* seems to represent an unspecialized group. The normal procedure of assaying characters for primitive conditions is by out-group comparison. Choosing a representative out-group for toadfishes is difficult. The characters we have used to separate species of *Batrachoides* are not useful in comparing *Batrachoides* with a more primitive paracanthopterygian group.

Based on meristic characters, there are four groups of species (Table 14). For vertebrae, dorsal and anal rays, the groups from high to low are: *boulengeri-surinamensis, waltersi-walkeri, pacifici-gilberti-liberiensis,* and *manglae-goldmani.* These meristic characters are positively correlated with each other and with maximum body size. To minimize the possibility of overweighting the analysis due to this correlation, we employed a metameric index. Species were placed in one of four arbitrary groups based on the location of the mode of each of three characters. Each species consistently scored the same index value for each of the three characters. Two other characters (numbers of pores in the upper and lower lateral lines) followed this same general trend: *boulengeri-surinamensis-waltersi*; *walkeri-pacifici*; and *manglae-goldmani. B. liberiensis* falls in with the latter group in upper lateral line pores and with *walkeri-pacifici* in lower lateral line pores.

Preliminary runs of the program produced rooted networks rather than phylogenetic trees. They utilized most of our data in which the characters were coded as either present or absent and no directionality was implied. The results of these runs were unacceptable. Character states were lost and reappeared several times within one phyletic lineage and several character states would have had to have been independently derived. Numbers of pectoral fin glands were useful in separating some species of *Batrachoides* from others but were not correlated with other characters. Specializations such as the pointed teeth and deeply divided swimbladder of *B. goldmani* distinguished this species but could not be used to suggest relationships.

B. walkeri and *B. liberiensis* presented special problems. They have intermediate metameric indices, being between species with low values (*B. manglae* and *B. goldmani*) and species with high values (*B. boulengeri* and *B. surinamensis*). Because the Wagner program constructs branches based on the most parsimonious conclusion and because *B. walkeri* and *B. liberiensis* are intermediate with respect to other species in metameric characters, use of characters which we now believe to be convergent (i.e., body size at maturity, presence or absence of

Table 14. Comparison of the species of *Batrachoides*

	boulengeri	*surinamensis*	*waltersi*	*walkeri*	*pacifici*	*gilberti*	*manglae*	*goldmani*	*liberiensis*
Maximum size (mm SL)	362	337	292	170	286	230	215	216	200
Eye size (% SL)	2.4–5.4	2.0–4.1	2.9–5.9	2.8	4.3–7.2	4.0–6.9	5.1–8.2	5.1–8.2	3.1–4.8
Eye in interorbital	2.4–5.9	2.0–6.2	1.5–4.1	3.3	0.8–2.6	0.9–2.5	0.6–1.8	0.6–2.0	1.8–3.4
Dorsal rays	28–30		26–28		24–27		21–23		24–26
Anal rays	25–27		23–25		21–23		19–21		21–23
Total vertebrae	37–39		35–37		34–36		31–33		33–35
Upper lateral line pores	52–68			40–52		28–42			
Lower lateral line pores	46–66			34–46		24–32			34–42
Pectoral glands	16–19	0–11	14–19	7–8	10–16	0–11		13–17	
Head squamation	mod.	extensive	mod.	min.	mod.		min.	mod.	
Interorbital filaments	none	ant.	few	none	few	mod.		many	
Supraorbital filaments	none			few	none	present	none	long	small
Teeth	blunt							pointed	blunt
Swimbladder	moderately divided							deeply	moderately

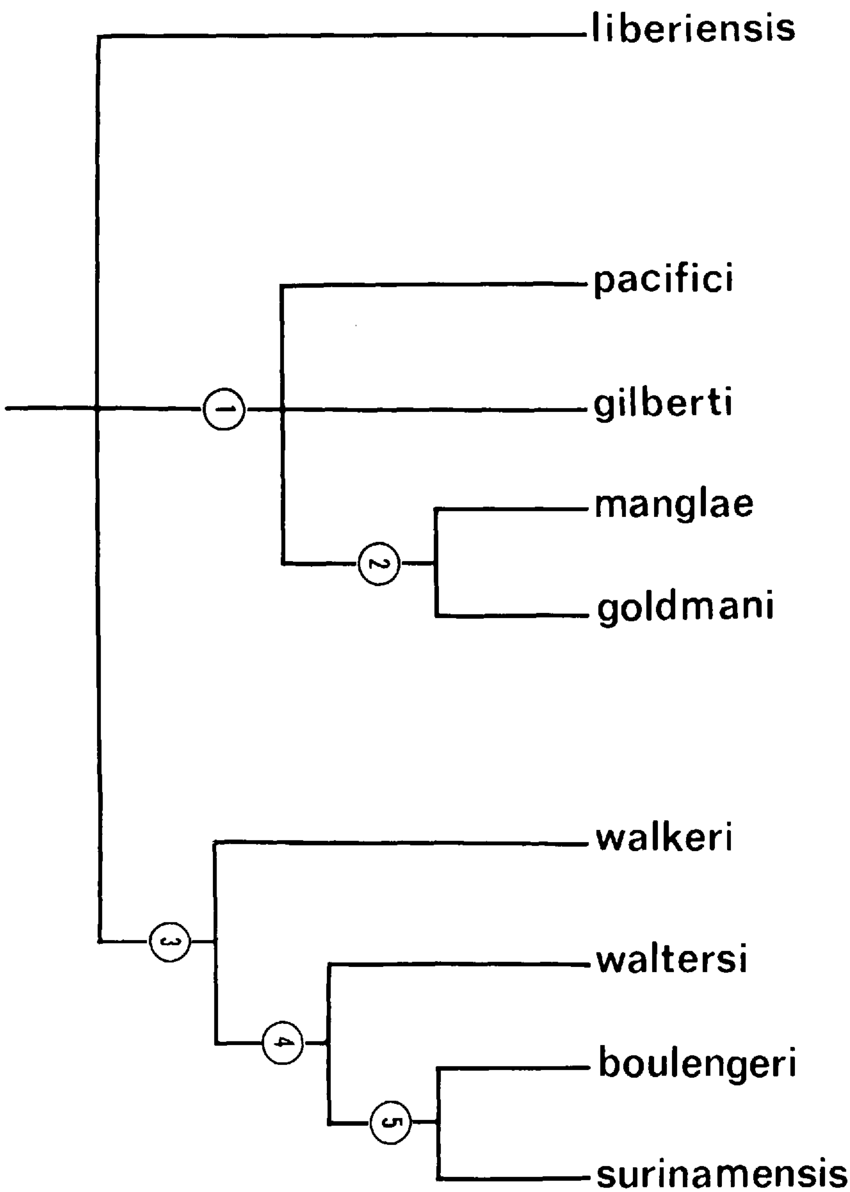

Figure 10. Cladogram of the nine species of *Batrachoides*. Shared characters at nodes: 1) increase in eye size, 2) decrease in metameric index, 3) increase in metameric index, 4) loss of interorbital filaments, 5) further increase in metameric index.

pectoral fin glands, interorbital distance) produced Wagner networks with numerous convergences. Deletion and addition of individual characters altered the branching sequence without reducing many of the convergences.

Use of the Wagner tree program and attempts to interpret the results of the first runs of the program forced us to more clearly define character states and to attempt to assign directionality to changes in states. We assumed that the first division within *Batrachoides* occurred between the Old and New worlds so we

could use one or the other as representative of a hypothetical ancestor. Since eight species of *Batrachoides* are represented in the New World and one (*B. liberiensis*) is found in the Old World (see zoogeography section), we have used *B. liberiensis* to represent the primitive condition. In squamation, number of opercular and subopercular spines, and absence of specialized filaments on the anterior nasal tube, *B. liberiensis* does seem more generalized than other eastern Atlantic toadfishes. If we make this assumption, it then follows that meristic characters have evolved in two directions in the New World—to lower counts in *B. manglae* and *B. goldmani* and to higher counts in *B. walkeri* and *B. waltersi* and still higher in *B. surinamensis* and *B. boulengeri*.

Two other characters are used in our analysis, large eyes, present in *B. pacifici, gilberti, manglae,* and *goldmani*; and loss of interorbital filaments in *B. boulengeri, surinamensis,* and *waltersi*. Small eye size is then viewed as a primitive character retained in the *boulengeri* line from *liberiensis* and loss of interorbital filaments as a specialization.

The program was run three times using the same data matrix. The first run produced a cladogram and rooted the tree at a hypothetical ancestor with its character states set at the primitive condition for each character. These were identical to *B. liberiensis*. The second run produced a Wagner network rooted at *B. liberiensis* and the third run rooted the network between the most divergent taxa. We were not surprised to find that the branching sequence of all three dendrograms was identical. Our phylogenetic conclusions are presented in a cladogram (Fig. 10). Resolution of the two unresolved trichotomies must await investigation of additional characters, such as osteological and biochemical and also a better definition of primitive versus specialized characters within *Batrachoides* and the Batrachoidinae.

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